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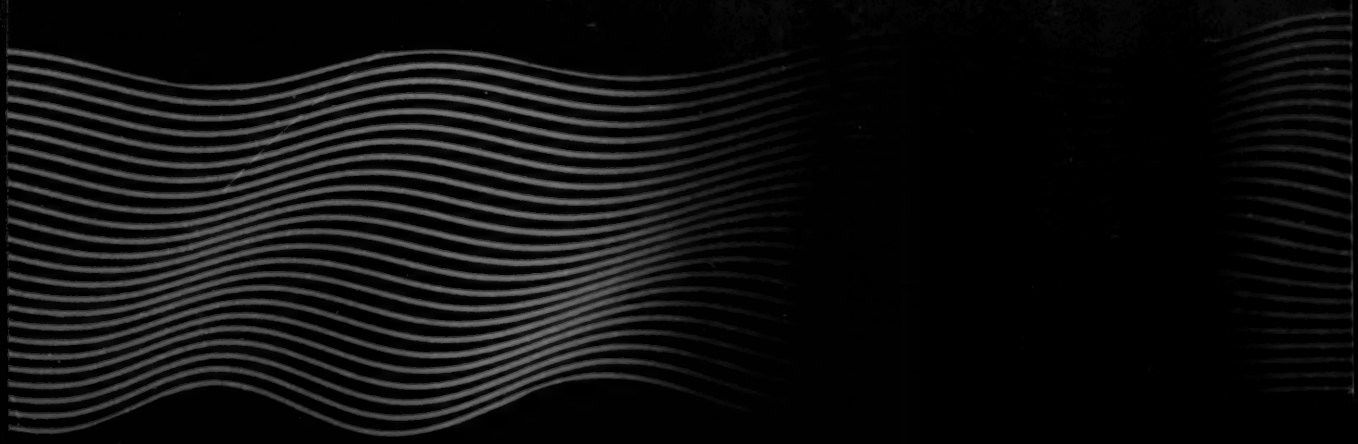

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Diel foraging cycles and interactions among juvenile Atlantic cod (*Gadus morhua*) at a nearshore site in Newfoundland

Scott M. Grant and Joseph A. Brown

Abstract: In coastal Newfoundland, age 0 Atlantic cod (*Gadus morhua*) settle in shallow, nearshore regions occupied by older conspecifics. Although intercohort cannibalism is common, little is known of the behavioural responses that limit interactions among juvenile cohorts in the wild. We examined the day–night differences in catch and diet of age 0 and age 1 cod to delineate peak foraging activity and resource use in eelgrass (*Zostera marina*) habitat. Cod exhibited a size-related shift (age 0 to age 1) from feeding predominantly on zooplankton by day to benthos at night. Intercohort cannibalism occurred when age 1 cod were approximately three times larger than their prey. Concentrations of age 0 cod foraged in the water column during the day, ceased feeding at night, and appeared to disperse to the bottom. Seasonally decreasing daylength and prey size contributed to a decline in daily ration, yet age 0 cod still maintained a strict diurnal foraging cycle. The nocturnal decrease in feeding coincided with an increase in the catch of older conspecifics (age 2 and age 3) and increased foraging activity of age 1 cod, suggesting that avoidance of older conspecifics is an important factor influencing the diel foraging and activity cycles of age 0 cod.

Résumé : Les morues de l'Atlantique (*Gadus morhua*) d'âge 0 des eaux côtières de Terre-Neuve se fixent dans les zones peu profondes du littoral où se trouvent déjà des morues plus âgées. Le cannibalisme intercohorte est courant, mais nous savons peu de choses des réponses comportementales qui limitent les interactions chez les cohortes de juvéniles à l'état sauvage. Nous avons examiné les écarts jour–nuit des prises et de la diète des morues d'âge 0 et 1 afin de déterminer les pics de la recherche de nourriture et de l'utilisation des ressources dans un habitat de zostère marine (*Zostera marina*). Nous avons noté un décalage lié à la taille (de l'âge 0 à l'âge 1) qui allait d'une consommation de phytoplancton le jour à une consommation d'animaux benthiques la nuit. Il y avait cannibalisme entre cohortes lorsque les poissons d'âge 1 étaient trois fois environ plus grands que leurs proies. Les morues d'âge 0 formant des concentrations se nourrissaient dans la colonne d'eau pendant le jour et, à la nuit, cessaient de s'alimenter et se dispersaient vers le fond. Le raccourcissement de la durée du jour dû à la saison et la taille des proies ont donné lieu à une baisse de la quantité de nourriture ingérée à chaque jour, mais les poissons d'âge 0 ont maintenu leur cycle d'alimentation strictement diurne. La diminution nocturne coïncidait avec un accroissement des prises de congénères plus âgés (âges 2 et 3) et à une augmentation de la recherche de nourriture des morues d'âge 1. Cela porte à croire que l'évitement des congénères plus âgés constitue un facteur important des cycles nycthéméraux de recherche de nourriture et d'activité des morues d'âge 0.
[Traduit par la Rédaction]

Introduction

Since the recent collapse of the North Atlantic cod (*Gadus morhua*) stock, young juveniles have largely been confined to coastal Newfoundland (Dalley and Anderson 1997). Coastal settlement of age 0 cod generally results in movement into areas occupied by older conspecifics (Clark and Green 1990; Methven and Bajdik 1994). One- to 3-year-old juveniles are typically found further away from shore during the day and show a nocturnal movement into shallow coastal waters where age 0 juveniles are concentrated (Pihl 1982; Riley and Parnell 1984; Clark and Green 1990; Keats 1990; Grant and Brown 1998; Methven and Schneider 1998). It has been suggested that this shoreward movement is associated with increased foraging activity by older fish (Pihl 1982). Intercohort cannibalism is common when small and large cod occur together (Bogstad et al. 1994), yet how small cod balance the trade-offs between when and where to forage and predation risk from older co-occurring conspecifics in coastal waters is not well understood. A better knowledge of the processes that reduce interactions between small fish and potential predators has broad ecological applications and will improve our understanding of the functional role of coastal habitats to the rebuilding of Atlantic cod stocks (Taggart et al. 1994)

Feeding requirements of rapidly growing, small fish often forces them to occupy the same habitat as larger potential predators. When distributions overlap, predator avoidance may be expected to have a greater effect on the foraging time and location of smaller individuals. Laboratory studies document a habitat shift by age 0 cod in the presence of actively foraging older conspecifics (Fraser et al. 1996), suggesting that the presence of older cod may influence the distribution and possibly the food intake of young cod in the wild.

Analysis of diet is a valuable tool for exploring interactions among fish. Mechanisms underlying changes in behaviour,

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distribution, and foraging activity such as predator avoidance may be reflected in diel or seasonal changes in diet. The presence of a predator may modify the foraging behaviour of small fish by inducing shoaling behaviour and (or) restricting feeding time and location (Lima and Dill 1990). High predation pressure could potentially result in decreased food intake and hence growth and survival.

The ecological significance of daily patterns of foraging in young juvenile cod has received little attention in coastal Newfoundland. In this study, we investigated diel and seasonal differences in catch and diet of age 0 and age 1 cod to delineate possible age-class differences in foraging behaviour and resource use in a preferred coastal habitat of age 0 cod. Seasonal changes in food intake were also established using field estimates of gastric evacuation and mean gut fullness over 24-h periods.

Materials and methods

Study location

This study was carried out at a shallow water site (about 5.5 m depth) in Goose Cove (47°50.5′N, 53°53.9′W), located in Bull Arm of Trinity Bay, Newfoundland, Canada. The substrate type at the study site consisted of sand and gravel and the bottom was dominated by a dense bed (about 75% cover) of eelgrass (*Zostera marina*) to a depth of about 5.0 m. A complete description of the study location is given in Grant and Brown (1998).

Diel variation in stomach contents

During the autumn of 1993, cod were collected at 3-h intervals over 24-h periods on September 13–14, October 4–5, and November 13–14 and at 4-h intervals on December 14–15. Sampling was carried out using one of two types of beach seine modified to fish 50 m from shore. Beach seine I (BS-I) had headrope and footrope lengths of 30 m and a stretched mesh size of 9 mm throughout. Beach seine II (BS-II) was first described by Lear et al. (1980) and had a 9-mm mesh size in the codend. Limited access to sampling gear required using BS-I during the September and December diel sampling program and BS-II during October and November.

The seines were deployed from a small boat (6 m) at a distance of 50 m from shore. During each set, the headropes were located at the same location on shore (16 m apart), thereby keeping the area sampled fairly constant (i.e., 800 m^2). The seine sampled the water column from the substrate to 2 m off the bottom.

Once the seine was brought to shore, fish were placed in a large tub filled with seawater and sorted by age-class. Up to 15 age 1 cod were immediately removed from the catch, followed by a sample of 10 age 0 cod. Fish were killed in anaesthetic (MS 222), placed on dry ice, and stored (–20°C) for later analysis. Water temperature was measured 50 m from shore, within 1.0 m of bottom.

In the laboratory, individual fish were thawed, blotted, and measured for standard length (SL, ±1.0 mm) and weight (±0.01 g). The stomach was removed and food items identified, counted, and weighed. Relative position of dominant prey within the stomach was recorded during dissection. There was no evidence of regurgitation. Preliminary analysis revealed that calanoid copepods dominated the diet of age 0 cod whereas larger invertebrates dominated the diet of age 1 cod. To assess diel changes in diet composition of age 0 cod with more precision, calanoid copepods were identified to genus or species. Harpacticoids in the diet of age 0 cod were combined to form a single taxon. All copepods were combined into a single taxon for age 1 cod. The remaining food types were identified to the same taxonomic level for both cod age-classes. For example, crustaceans were identified to order, annelids to class, gastropods and pelecypods pooled into Mollusca, and fish were considered a single group.

Food items in the stomach of individual age 0 cod were separated into one of the taxa outlined above, placed on a glass filter, and dried to a constant weight (± 10 µg) at 80°C. Unidentified food material was treated in a similar manner.

Due to the predominance of larger food items in the diet, the method used to obtain the total weight contribution of small zooplankton differed for age 1 cod. Small zooplankter taxa, specifically copepods, cladocerans, and pelecypod veligers, were counted for each fish. An average weight was estimated for each zooplankter taxon by pooling a random sample of up to 200 individuals from no fewer than three cod. The remaining zooplankters from each stomach were then pooled with the unidentifiable food material from that stomach. Larger food items in each stomach were separated and grouped into one of the taxa outlined above. Food groups, identified for each fish, were dried separately to a constant weight (± 100 µg) at 80°C. For each diel sampling program, the total weight contribution of copepods, cladocerans, and pelecypod veligers to the diet of each age 1 cod was estimated from the average weight and number of individuals counted. The weight of unidentifiable food material was obtained by difference.

An index of relative importance (IRI), developed by George and Hadley (1979), was used to estimate the importance of each prey taxon in the diet of age 0 and age 1 cod. The IRI is derived from an index of absolute importance that combines three standard diet measures (percent frequency of occurrence, percent total number, and percent total weight) into a single index for each taxon.

To account for variation in body size, weight of the stomach contents at time t was weighed for fish size by establishing an index of gut fullness, expressed as

$$(1) \qquad C_t = \frac{G_t}{W_t} \times 100 \text{ (grams dry per 100 g wet)}$$

where G_t is the dry weight of the stomach contents (grams) and W_t is the total wet body weight (grams). The average gut fullness at time t was estimated by including fish with empty stomachs.

Gastric evacuation and daily ration

Exponential rates of gastric emptying have been described for young cod (Tyler 1970), and the exponential model has been identified as giving the best description of the rate of gastric evacuation (R, per hour) of fish, particularly when fish are feeding on small food items (Jobling 1986). The exponential model defines gastric evacuation as

$$(2) \qquad \overline{C}_x = \overline{C}_0 e^{-RT}$$

where $\overline{C}_0$ and $\overline{C}_x$ are, respectively, the average gut fullness at the beginning and end of time interval T (3–4 h) and R is the instantaneous evacuation rate. In its logarithmic form, eq. 2 is written as

$$(3) \qquad \ln\overline{C}_x = \ln\overline{C}_0 - RT$$

The evacuation rate was estimated for age 0 and age 1 cod for each diel survey as the slope of the relationship between $\ln \overline{C}_0$ and time. This was accomplished by identifying the greatest peak in gut fullness for a diel survey and calculating R over the subsequent series of observations where $\overline{C}_x < \overline{C}_0$.

Daily ration was determined using the Eggers (1977) model which assumes an exponential evacuation function to estimate the average daily ration of all fish collected during a given day ($\overline{D}$, grams dry per 100 g wet per day). The Eggers model defines daily ration as

$$(4) \qquad \overline{D} = \overline{C} \times R \times 24$$

where $\overline{C}$ is the average gut fullness of all fish collected over a 24-h period, R is the prevailing gastric evacuation rate, and 24 is the number of hours in a day.

Eggers (1979) suggested that daily ration values derived from his model may be biased when the stomach contents at the beginning and end of a 24-h period are not equal. Therefore, we performed a t-test

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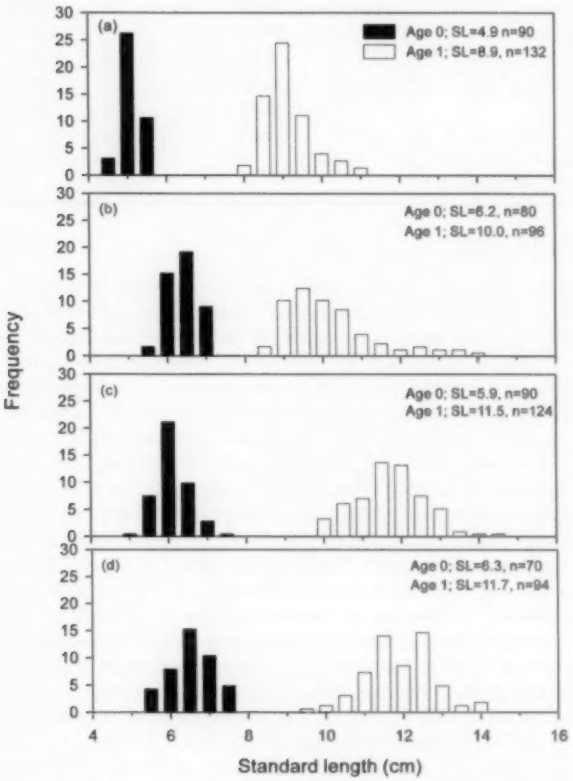
Fig. 1. Length–frequency distributions for each of age 0 and age 1 Atlantic cod in Goose Cove, Newfoundland, for (*a*) September, (*b*) October, (*c*) November, and (*d*) December 1993. Average length (SL, cm) and total number (*n*) of each age-class are also shown.



on the difference between gut fullness of C_0 and C_{24} to verify if Eggers' (1979) correction should be used.

Results

Size and catch of juvenile cod

The size of age 0 cod retained for analysis in this study ranged from 4.2 to 7.4 cm SL and of age 1 cod ranged from 7.9 to 14.3 cm SL (Fig. 1). Larger conspecifics ranged from 16.6 to 27.5 cm SL and corresponded to age 2 and age 3 cod (May et al. 1965; i.e., age >1, Table 1). Age 0 cod dominated the autumnal catch in Goose Cove and the mean catch of this age-class was always highest during the day (Table 1). Conversely, 2- and 3-year-old cod were rarely captured during the day but were well represented at night, which is when the mean catch was highest. The mean catch of age 1 cod did not show a consistent diel pattern. Day–night differences in the mean catch of each juvenile cod age-class were assessed using a randomization test (Siegel 1956). Mean catch differed between all light periods tested for age 0 cod (September, $p = 0.016$; October, $p = 0.018$; November, $p = 0.008$; December, $p = 0.029$) and all but one (October) for age >1 cod (September, $p = 0.008$; October, $p = 0.286$; November, $p = 0.024$; December, $p = 0.029$). Mean catch of age 1 cod was higher at night in September ($p = 0.016$) but did not differ between light periods in October ($p = 0.686$), November ($p = 0.317$), or December ($p = 0.371$).

In addition to juvenile cod, four other fish species (*Gadus ogac*, *Gasterosteus aculeatus*, *Pleuronectes americanus*, and *Myoxocephalus scorpius*) were also recorded in the catches. Of these four species, *G. ogac* was most prevalent. When very small, *G. morhua* and *G. ogac* are morphologically similar; however, these two species can be distinguished at a size of about 4.0–5.0 cm SL (i.e., differences in anal fin pigmentation; S. Grant, unpublished data).

Two temporally spaced autumnal influxes (i.e., August–September and October–November) of small (3.5–6.0 cm) recently settled age 0 cod have been reported in coastal Newfoundland (Methven and Bajdik 1994). Our study confirms these findings, and high numbers of recently settled cod were also observed in our catches during December (Fig. 1), indicating that in some years, nearshore settlement may extend beyond November. Age 0 *G. ogac* were also captured in Goose Cove; however, they appear to settle only in August–September.

Diel feeding cycle and diet composition

Mean gut fullness of age 0 cod showed a marked diel cycle that did not vary during the autumn months (Fig. 2). Mean gut fullness increased throughout the day, peaked at dusk, and declined until dawn, when cod resumed feeding. Mean gut fullness at dusk ranged from 0.16 to 1.09 for December and October, respectively (Fig. 2). The proportion of fish with empty stomachs peaked at the end of the nocturnal period, suggesting that cod did not feed at night. Stages of food digestion also provide evidence that age 0 cod did not feed at night. For example, after sunset, the anterior region of the stomach became constricted, and as digestion progressed, food formed a bolus in the posterior region of the stomach. Only the central region of the bolus contained identifiable prey items, suggesting a peripheral action of digestion.

Throughout autumn, the diet of age 0 cod was dominated by small (<4 mm) crustacean zooplankton (Fig. 3). To obtain an unbiased estimate of the seasonal variation in zooplankter importance, an IRI was calculated for all cod captured during the day, which was when fish were actively feeding (Table 2). Cladocerans (*Podon* sp. and *Evadne* sp.) dominated the diet during September, followed largely by copepodite stages of *Acartia* sp. and pelecypod veligers. These zooplankters were very small (<1 mm). Cladocerans maintained a moderate importance to the diet through November. During October, pelecypod veligers and *Acartia* sp. were replaced by larger calanoid genera (1.5–4.0 mm). Larger adult stages of *Temora longicornis* dominated in October and *Calanus finmarchicus*, particularly copepodites with a high incidence of oil sacs, were also important. Increased importance of small zooplankters, copepodites of *Pseudocalanus* sp. and *Acartia* sp., during November and December coincided with an increase in the consumption of small copepodite stages of all calanoids.

Benthic and epibenthic prey were generally of minor importance to the diet of age 0 cod (Fig. 3). Cumaceans were the largest prey items consumed (<9 mm). Small benthic (gammarid) and pelagic (hyperiid) amphipods (<7 mm) were also consumed as well as epibenthic harpacticoids (<3 mm). All

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Table 1. Diel variation in the catch (number per haul) of juvenile Atlantic cod in Goose Cove, Newfoundland, during autumn 1993.

September				October				November				December			
Time	Age 0	Age 1	Age >1	Time	Age 0	Age 1	Age >1	Time	Age 0	Age 1	Age >1	Time	Age 0	Age 1	Age >1
08:00	393	16	0	16:00	106	5	2	09:00	379	13	1	16:00	181	13	0
11:00	803	17	0	19:30*	24	13	1	12:00	237	11	0	20:00*	30	16	3
14:00	418	12	0	22:00*	38	19	5	15:00	494	12	0	24:00*	18	13	4
17:00	569	15	0	01:00*	13	13	7	18:00*	76	20	1	04:00*	19	8	6
20:00*	75	21	2	04:30*	15	19	2	21:00*	48	18	4	08:00	437	17	0
23:00*	43	26	8	07:00*	35	7	3	24:00*	41	19	5	12:00	252	14	0
02:00*	47	29	3	10:00	200	38	2	03:00*	64	13	3	16:00	295	15	0
05:00*	59	24	5	13:00	146	20	1	06:00*	44	15	3				
08:00	287	20	0					09:00	346	21	0				

*Nocturnal collection.

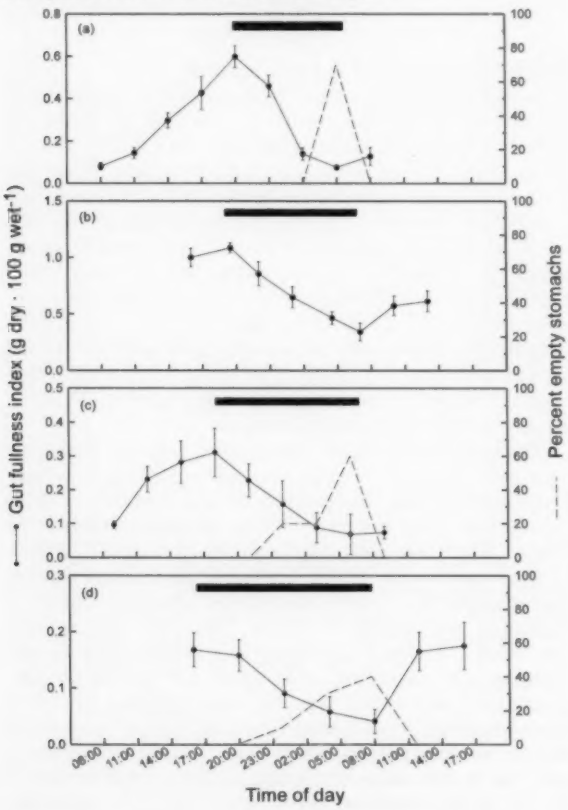

Fig. 2. Diel variation in the gut fullness of age 0 Atlantic cod sampled in Goose Cove, Newfoundland, during (*a*) September, (*b*) October, (*c*) November, and (*d*) December 1993. Error bars represent the 95% CI for 10 cod. Note that the left vertical axes are not equal. Solid horizontal bars indicate night.

amphipods found in the diet during September were pelagic and small (2–3 mm). For the remaining months, it was generally observed that pelagic amphipods were consumed during the day whereas benthic amphipods and cumaceans were consumed at dusk and dawn, suggesting a benthic association of age 0 cod at night. After sunset, benthos was observed in the anterior region of the stomach, and as digestion progressed, these larger prey were typically found in the centre of the gastric bolus, being surrounded by partially digested food.

Distinct changes in the position of dominant zooplankton taxa in the stomachs of age 0 cod appeared to correspond to changes in the tidal current, suggesting a tidal influence on feeding behaviour. For example, on September 13, low and high tide occurred at about 10:00 and 16:30, respectively. Position in the stomach revealed that cladocerans and pelecypod veligers were largely consumed during ebb tide whereas *Acartia* sp. were consumed during flood tide. At 08:00, cladocerans and pelecypod veligers dominated the diet (Fig. 3). By 11:00, *Acartia* sp. dominated the anterior region of the stomach and exhibited an increase in dietary importance throughout the flood tide. During flood tide, cladocerans and pelecypod veligers were found in the posterior region of the stomach of all fish sampled. At 17:00, cladocerans and pelecypod veligers dominated the anterior region of the stomach and showed an increase in importance throughout the ebb tide (Fig. 3). On November 13, low and high tide were at about 13:15 and 19:00, respectively. The position of dominant prey in the stomach revealed that *Pseudocalanus* sp., *Acartia* sp., and cladocerans were consumed during ebb tide whereas *T. longicornis* and *C. finmarchicus* were consumed during flood tide. These observations were supported by diel changes in the importance of these prey types (Fig. 3). In October, *T. longicornis* and cladocerans generally dominated the anterior region of the stomach during ebb tide. However, we could not establish distinct trends on the influence of tide on feeding during October and December, which we attribute to the distinct diurnal foraging cycle of age 0 cod and the initiation of these diel surveys during late afternoon (Fig. 2).

Age 1 cod fed predominantly at night (Fig. 4). However, prey items in fresh condition were observed throughout the diel period, suggesting that intake was not zero when $\overline{C}_x < \overline{C}_0$. Mean gut fullness showed a single nocturnal peak at about 2 h of midnight in September, October, and December. In November, two nocturnal peaks in gut fullness were observed: one after sunset and a second before sunrise. Peaks in mean gut fullness ranged from 0.72 to 1.18 in December and October, respectively (Fig. 4). Overall, the highest proportion of fish with empty stomachs was observed during the day.

Small crustacean zooplankton were of minor importance to the diet of age 1 cod in September, peaked in importance during October, and were of limited importance during November

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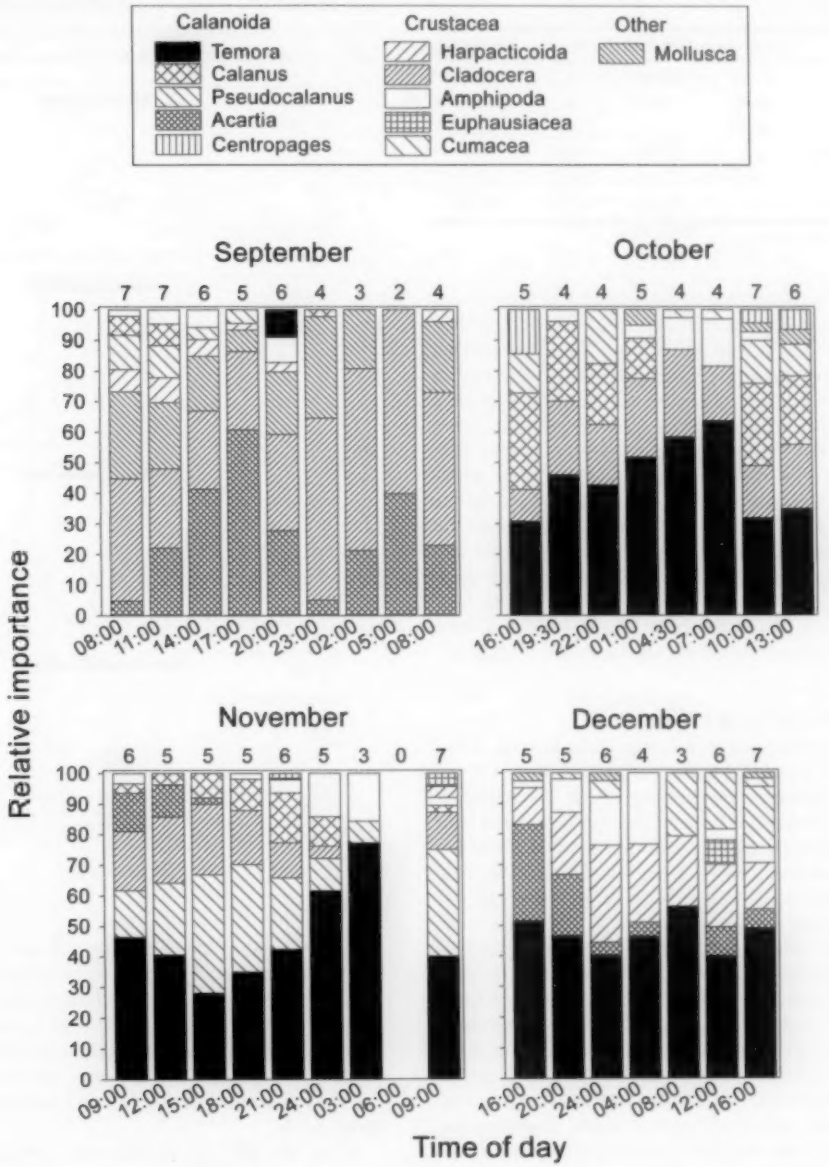
Fig. 3. Diel variation in the relative importance of prey taxa in the diet of age 0 Atlantic cod sampled in Goose Cove, Newfoundland, September–December 1993. The number of prey taxa identified at each sampling event is indicated above each bar.



and December (Fig. 5). Greatly increased predation is commonly associated with increased prey abundance (Keast 1977) and fish select the largest zooplankters (Noble 1975). The sharp increased in importance of copepods to the diet of age 1 cod in October coincided with a sudden switch to large copepods by age 0 cod, providing evidence of an increase in the abundance of large zooplankters.

Mysids and gammarid amphipods dominated the diet of age 1 cod during September, November, and December, and increased importance of mysids (Fig. 5) was associated with peaks in mean gut fullness (Fig. 4). Even the October peak in gut fullness (Fig. 4) resulted from a few cod (40%) that had consumed a large quantity of mysids, indicating that increased foraging activity was associated with the nocturnal consumption of large benthic prey.

During November and December, seven cod stomachs contained fish. State of digestion indicated that these fish were not consumed during capture. Five cod consumed fish that were identifiable as age 0 cod. The lengths (centimetres) of the age 0 cod and age 1 cannibals (in parentheses) were as follows: 4.0 (11.6), 4.2 (12.4), 4.4 (12.3), 4.7 (13.9), and 5.0 (13.6). Age 1 cannibals were on average 2.9 times larger (2.7–3.0 times) than

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Table 2. Relative importance of dominant zooplankton taxa to the diurnal diet of age 0 Atlantic cod in Goose Cove, Newfoundland, during autumn 1993.

Taxon	September	October	November	December
Cladocera	37.74	18.08	18.72	—
Pelecypod veligers	21.89	—	—	—
Acartia sp.	22.87	—	—	12.40
Calanus finmarchicus	—	21.47	5.83	—
Pseudocalanus sp.	—	7.11	29.63	14.98
Temora longicornis	—	41.38	37.96	48.26

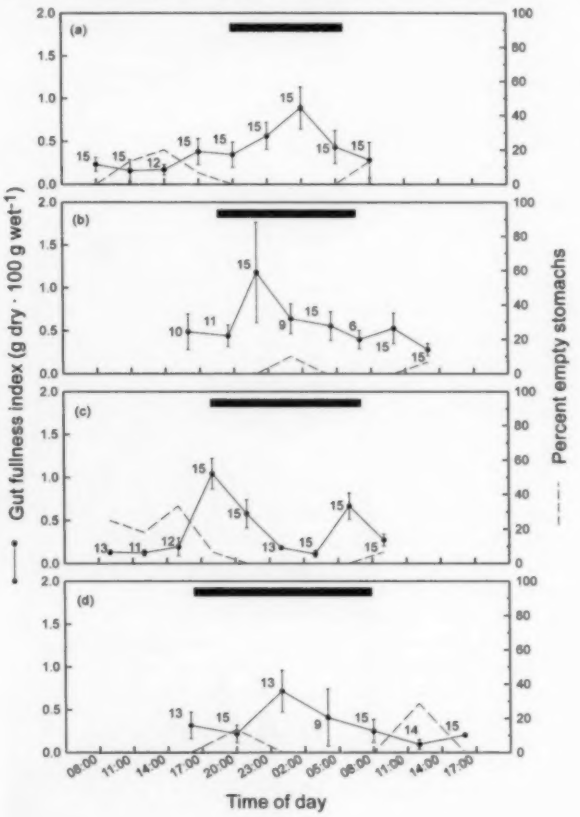
Note: Values >5% are shown.

their prey. This is in agreement with findings that suggest that piscivorous fish must be at least three to four times larger then their prey (Nursall 1973; Bogstad et al. 1994). The smallest cod collected during this study was 4.2 cm; however, cod as small as 2.2 cm SL have been captured in nearshore surveys that utilized the same gear (S. Grant, personal observation). It therefore seems reasonable to assume that age 1 cod were consuming the smallest cod available (i.e., 4.0 cm). Further analysis of our data revealed a marked seasonal increase in the proportion of age 1 cod that were ≥2.9 times larger than the smallest cod consumed (September, 0.7%; October, 11.4%; November, 50.0%; December, 59.6%). The number of age 0 cod in the diet of age 1 cod in November and December corresponds to 1.6 and 7.1%, respectively, of age 1 cod that were large enough and had consumed the smallest cod available.

Gastric evacuation and daily ration

Field estimates of gastric evacuation rates ranged from 0.092 to 0.248·h^{-1} for age 0 cod and from 0.111 to 0.258·h^{-1} for age 1 cod (Table 3). In principle, measuring gastric evacuation in the field is the ideal situation because the fish have been subjected to natural environmental conditions and diet (Bromley 1994). In the present study, the fish exhibited distinct feeding cycles with clearcut peaks in gut fullness, patterns that are suitable for estimating gastric evacuation in the wild. However, prey size may influence evacuation rate (Bromley 1994) such that field estimates of gastric evacuation may be confounded by high variance in diet composition and when feeding occurs between samples where $\overline{C}_x < \overline{C}_0$. These factors may have had little influence on estimates of gastric evacuation for age 0 cod. Age 0 cod showed little seasonal variation in diet composition, feeding mainly on small crustacean zooplankton, and food intake was apparently zero at night. However, increased diet diversity and variation in stomach contents (composition and weight) that accompanied an increase in body size suggest that the true evacuation rate was underestimated for age 1 cod. Fresh food items were found in the diet of age 1 cod throughout the 24-h surveys and individual cod exhibited differences in feeding. Additionally, the proportion of the age 1 cod population feeding on larger prey was small at times. As such, the probability of the succeeding samples containing fish that had fed on the same prey in equal proportion may also be small. Evidence of differing feeding frequencies (two versus a single nocturnal peak in gut fullness) and the possibility of differing individual evacuation rates for age 1 cod that shift to larger prey is likely to lead to errors in estimating evacuation rate in the wild.

Fig. 4. Diel variation in the gut fullness of age 1 Atlantic cod sampled at Goose Cove, Newfoundland, during (*a*) September, (*b*) October, (*c*) November, and (*d*) December 1993. Values to the left of each symbol represent the number of cod sampled and error bars represent the 95% CI. Solid horizontal bars indicate night.



Gut fullness at the beginning and end of a 24-h survey did not differ significantly for either juvenile age-class ($p > 0.05$). Therefore, eq. 4 was used to estimate daily ration. The October diel survey only accounted for a 21-h period (16:00–13:00). Since C_0 and C_{24} showed no significant difference during September, November, and December, we assumed that these values were also equal during October and calculated daily ration using eq. 4.

Even though age 0 cod were consuming considerably smaller zooplankters in September, mean daily ration was comparable to that observed in October when both age-classes increased their consumption of large zooplankton, suggesting that zooplankter abundance was high early in the season. The October–November decrease in consumption of large copepods by age 0 cod coincided with a 2.7-fold decrease in mean daily ration (Table 3). Ration size and the size of the zooplankters consumed continued to decline to December, suggesting a seasonal decline in the size and abundance of zooplankters. The seasonal decline in daily ration also coincided with a decrease in water temperature (Table 3) and daylength. There were no seasonal trends in the average daily ration of age 1 cod.

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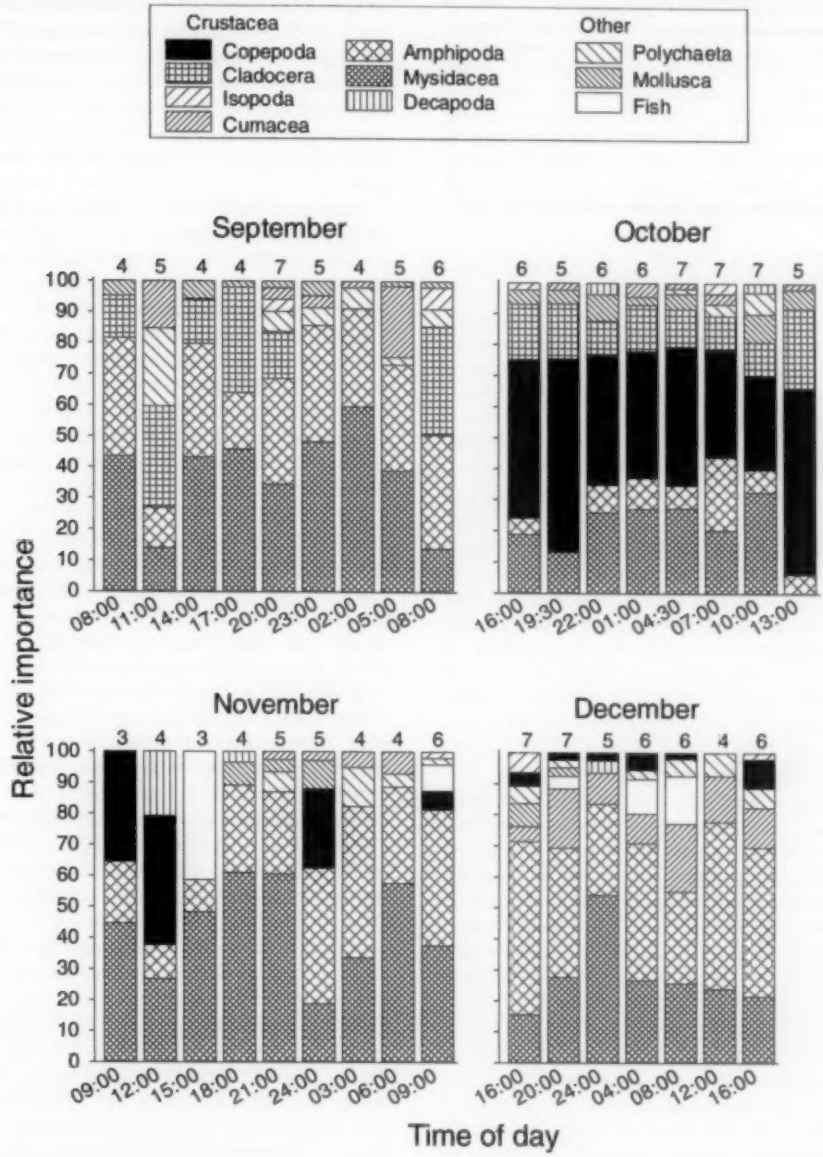
Fig. 5. Diel variation in the relative importance of prey taxa in the diet of age 1 Atlantic cod sampled in Goose Cove, Newfoundland, September–December 1993. The number of prey taxa identified at each sampling event is indicated above each bar.



Discussion

In this study, age 0 cod exhibited a distinct diurnal foraging cycle that contrasts the nocturnal foraging cycle exhibited by pelagic juveniles of similar size in the North Sea (Robb 1981). In addition, a seasonal decline in daylength and size of zooplankton consumed contributed to a decrease in food intake, yet age 0 cod still maintained a strict diurnal foraging cycle and zooplanktivory. This is surprising, as twilight consumption of benthos indicates that some of the benthos falls within the size limits of prey that age 0 cod can successfully handle and consume, and the nocturnal consumption of benthos and small crustacean zooplankton by age 1 cod indicates that these prey were available at night. It is well documented that trade-offs between food availability and predation risk can affect where and when young fish decide to feed (Lima and Dill 1990). We suggest that age 0 cod move to protective bottom cover, cease feeding, and become less active in coastal regions at night to reduce interactions with potential predators, in this case, older conspecifics. Recent laboratory studies have shown that age 0 cod shift habitat and seek shelter to reduce predation mortality from actively foraging older conspecifics (Fraser et al. 1996; Gotceitas et al. 1997), and movement by age 0 cod into very shallow-water sites at night (i.e., <1.2 m;

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Table 3. Field estimates of gastric evacuation rate (R, h^{-1}) and average daily ration ($\bar{D}$, g dry·100 g wet^{-1}·day^{-1}) of age 0 and age 1 Atlantic cod at different autumnal water temperatures (T, °C).

		Age 0		Age 1	
	T	R	$\bar{D}$	R	$\bar{D}$
September	12.8	0.248	1.65	0.191	1.82
October	9.1	0.095	1.56	0.114	1.54
November	6.0	0.132	0.57	0.258	2.36
December	3.7	0.095	0.26	0.164	1.32

Methven and Bajdik 1994) may also be in response to increased predation risk. Current findings indicate a lack of nocturnal feeding by age 0 cod, which coincided with an increase in the catch of 2- and 3-year-old conspecifics and increased foraging activity of 1-year-old cod, suggesting that avoidance of older conspecifics is an important factor influencing the diel foraging and activity cycle of age 0 cod.

Periodic influxes of high numbers of newly settled cod, which appear to remain localized within coastal areas for several weeks (Grant and Brown 1998), may be the stimulus that attracts older conspecifics into shallow-water regions at night (Clark and Green 1990; Keats 1990; Methven and Bajdik 1994). Pihl (1982) noted that twilight foraging by large juvenile cod may be more pronounced in coastal populations, and increased activity at dusk and dawn by 2- and 3-year-old cod appears to be associated with a migration into and out of shallow-water regions (Clark and Green 1990). Intercohort cannibalism is common in cod and increases with predator length, density of young cod, and degree of overlap in distributions (Bogstad et al. 1994). Bogstad et al. (1994) documented that almost all cannibalism in cod was by fish that were at least twice the length of their prey and that most were more than three times longer. This study corroborates these findings, as there was no evidence of cannibalism by 1-year-old cod until at least 50% of the fish sampled had attained a size about three times larger than newly settled cod. It is important to note that cod within a size range of 8–10 cm shifted from feeding predominantly on small zooplankton by day to large benthic invertebrates at night. A similar size-related shift to benthos was also reported in neighbouring Conception Bay, Newfoundland (Keats et al. 1987). However, this is the first documented case of a size-related shift to nocturnal foraging in juvenile cod which suggests that larger fish accrue a size benefit and are likely above the upper limit of prey size for nocturnal predators. Apart from the prevalence of older conspecifics, studies in nearshore regions of Newfoundland document low bycatch of potential predators on small juvenile cod (Gotceitas et al. 1997; this study). If cannibalism does play a major role in the survival of newly settled cod in nearshore regions of Newfoundland, then coastal nursery grounds may contribute little to the population in years/locations where abundance of older juveniles is high.

Capture rate and dietary studies of fish based on samples collected irrespective of time of day are limited to reporting the presence of fish and prey importance to the diet at one moment in time. As such, these studies provide little insight into diel changes in distribution and activity which may ultimately be related to varying local environmental factors. Current findings document a size-related shift in foraging time and location by young juvenile cod, which may be explained by differential predation risk associated with an increase in the shoreward movement (Clark and Green 1990; Keats 1990) and foraging (Pihl 1982) by older conspecifics at night. These day–night differences in distribution and activity by juvenile cod in shallow nearshore waters are apparently size related and imply that population-based studies (intercohort) on relative abundance and (or) extent of cannibalism may not be accurately determined by a common (i.e., diurnal) sampling frequency.

Age 0 cod may be highly concentrated in nearshore regions of Newfoundland (Lear et al. 1980) and maintain localized populations (Grant and Brown 1998), and the presence of eelgrass appears to be an important factor influencing their nearshore distribution throughout the North Atlantic (Tveite 1984; Tupper and Boutilier 1995; Gotceitas et al. 1997; Grant and Brown 1998). Studies suggest that small juvenile cod are associated with habitats that exhibit increased bottom structure due to the protection that these areas provide from predators (Tupper and Boutilier 1995; Gotceitas et al. 1997). However, suitable habitat must also provide an adequate supply of food. A recent study has identified strong tidal currents at our study site in Goose Cove (S.M. Grant and B. de Young, unpublished data), and our results on diet composition suggest a tidal-related feeding pattern. We suggest that high concentrations of newly settled age 0 cod may also be associated with coastal areas that exhibit physical features that intensify water currents and serve to concentrate zooplankton. The use of food progression in the stomach to ascertain feeding time is not uncommon (Webster 1942); however, in the present study, the importance of the tidal cycle to diet composition was not discovered until after sampling was completed. To test the hypothesis of tidal-related feeding, additional data would have to be collected over more than one 24-h period and preferably on days when the change in tidal flood occurs at different times of the day.

Planktivorous fish are size selective, exhibiting a preference for larger prey items, and a decrease in zooplankton size and abundance may result in decreased growth (Goodlad et al. 1974; Noble 1975). In neighbouring Conception Bay, Newfoundland, Davis (1982) documented a late summer – early autumn decrease in size and abundance of the same copepods that dominated the diet of age 0 cod in this study. Our results on diet composition and daily ration of age 0 cod were also indicative of an autumnal decrease in size and abundance of the copepod resource, suggesting that cod settling late in the season in coastal regions of Newfoundland may be food limited. Higher water temperature, increased daylength, and evidence of increased size and abundance of zooplankton suggest cod that settle early may grow quicker and shift to feeding on larger prey, thereby increasing their growth efficiency (Kerr 1971) before winter. Many fish species overwinter on stored energy reserves, and in temperate climates, overwintering mortality is high for very small individuals (Henderson et al. 1988). Cod that settle early are likely in better condition for surviving the first winter and may reach a size where they prey on smaller cod that settle late (intracohort cannibalism). Intracohort cannibalism has been reported in age 0 cod off Iceland (Bogstad et al. 1994). Small body size of age 0 cod resulted in cannibalism by age 1 cod, and both age-classes overwinter in coastal regions of Newfoundland (Methven and Bajdik 1994; Grant and Brown 1998), suggesting that predation mortality

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may also result in a reduction in overwintering survival of age 0 cod that settle late.

Physical disturbance caused by sampling can affect habitat structure and the distribution and behaviour of mobile animals. Our results on the diel feeding of age 0 and age 1 cod indicate distinct diurnal and nocturnal peaks, respectively, in stomach content weight throughout the season, and these peaks were each associated with the consumption of the same prey types (i.e., zooplankton and benthos, respectively) by each cohort. We conclude that repeat sampling at the same site had little influence on the diel behaviour of the predators and their prey.

In summary, our results supply evidence that age 0 cod reduce potential interactions with larger 1- to 3-year-old conspecifics through diel differences in foraging and distribution in shallow nearshore waters. Nocturnal avoidance of older conspecifics may indirectly contribute to a seasonal decrease in foraging success (daily ration) and hence growth and survival, particularly for age 0 cod that settle late in the season when daylength and temperatures are reduced. This study documents intercohort cannibalism by 1-year-old cod and provides indirect evidence that the nocturnal increase in abundance of 2- and 3-year-old cod in shallow coastal waters of Newfoundland is related to high local densities of newly settled juveniles. The extent of cannibalism in shallow nearshore regions and its potential for directly or indirectly influencing cod recruitment warrant further investigation.

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References

Bogstad, B., Lilly, G.R., Mehl, S., Pálsson, Ó.K., and Stefánsson, G. 1994. Cannibalism and year-class strength in Atlantic cod (*Gadus morhua* L.) in Arcto-boreal ecosystems (Barents Sea, Iceland, and eastern Newfoundland). ICES Mar. Sci. Symp. **198**: 576–599.

Bromley, P.J. 1994. The role of gastric evacuation experiments in quantifying the feeding of predatory fish. Rev. Fish Biol. Fish. **4**: 36–66.

Clark, D.S., and Green, J.M. 1990. Activity and movement patterns of juvenile Atlantic cod, *Gadus morhua*, in Conception Bay, Newfoundland, as determined by sonic telemetry. Can. J. Zool. **68**: 1434–1442.

Dalley, E.L., and Anderson, J.T. 1997. Age-dependent distribution of demersal juvenile Atlantic cod (*Gadus morhua*) in inshore/offshore northeast Newfoundland. Can. J. Fish. Aquat. Sci. **54**(Suppl. 1): 168–176.

Davis, C.C. 1982. A preliminary quantitative study of the zooplankton from Conception Bay, insular Newfoundland, Canada. Int. Rev. Gesamten Hydrobiol. **67**: 713–747.

Eggers, D.M. 1977. Factors in interpreting data obtained by diel sampling of fish stomachs. J. Fish. Res. Board Can. **34**: 290–294.

Eggers, D.M. 1979. Comments on some recent methods for estimating food consumption by fish. J. Fish. Res. Board Can. **36**: 1020.

Fraser, S., Gotceitas, V., and Brown, J.A. 1996. Interactions between age classes of Atlantic cod and their distribution among bottom substrates. Can. J. Fish. Aquat. Sci. **53**: 305–314.

George, E.L., and Hadley, W.F. 1979. Food and habitat partitioning between the rock bass (*Ambloplites rupestris*) and smallmouth bass (*Micropterus dolomieui*) young of the year. Trans. Am. Fish. Soc. **108**: 253–261.

Goodlad, J.C., Gjernes, T.W., and Brannon, E.L. 1974. Factors affecting sockeye salmon (*Oncorhynchus nerka*) growth in four lakes of the Fraser River system. J. Fish. Res. Board Can. **31**: 871–892.

Gotceitas, V., Fraser, S., and Brown, J.A. 1997. Use of eelgrass beds (*Zostera marina*) by juvenile Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **54**: 1306–1319.

Grant, S.M., and Brown, J.A. 1998. Nearshore settlement and localized populations of age 0 Atlantic cod (*Gadus morhua*) in shallow coastal waters of Newfoundland. Can. J. Fish. Aquat. Sci. **55**. This issue.

Henderson, P.A., Holmes, R.H.A., and Bamber, R.N. 1988. Size-selective overwintering mortality in the sand smelt, *Atherina boyeri* Risso, and its role in population regulation. J. Fish Biol. **33**: 221–233.

Jobling, M. 1986. Mythical models of gastric emptying and implications for food consumption studies. Environ. Biol. Fishes, **16**: 35–50.

Keast, A. 1977. Diet overlaps and feeding relationships between the year classes in the yellow perch (*Perca flavescens*). Environ. Biol. Fishes, **2**: 53–70.

Keats, D.W. 1990. A nocturnal inshore movement of juvenile cod *Gadus morhua* L. in eastern Newfoundland. J. Exp. Mar. Biol. Ecol. **139**: 167–173.

Keats, D.W., Steele, D.H., and South, G.R. 1987. The role of fleshy macroalgae in the ecology of juvenile cod (*Gadus morhua* L.) in inshore waters off eastern Newfoundland. Can. J. Zool. **65**: 49–53.

Kerr, S.R. 1971. Prediction of fish growth efficiency in nature. J. Fish. Res. Board Can. **28**: 809–814.

Lear, H.M., Fleming, A.M., and Wells, R. 1980. Results of small cod surveys in eastern Newfoundland during 1959–1964. NAFO. SCR Doc. 80/IX/144, No. N218. pp. 1–8.

Lima, S.L., and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. **68**: 619–640.

May, A.W., Pinhorn, A.T., Wells, R., and Fleming, A.M. 1965. Cod growth and temperature in the Newfoundland area. Int. Comm. Northwest Atl. Fish. Spec. Publ. No. 6. pp. 545–555.

Methven, D.A., and Bajdik, C. 1994. Temporal variation in size and abundance of juvenile Atlantic cod (*Gadus morhua*) at an inshore site off eastern Newfoundland. Can. J. Fish. Aquat. Sci. **51**: 78–90.

Methven, D.A., and Schneider, D.C. 1998. Gear-independent patterns of variation in catch of juvenile Atlantic cod (*Gadus morhua*) in coastal habitats. Can. J. Fish. Aquat. Sci. **55**. This issue.

Noble, R.L. 1975. Growth of young yellow perch (*Perca flavescens*) in relation to zooplankton populations. Trans. Am. Fish. Soc. **104**: 731–741.

Nursall, J.R. 1973. Some behavioural interactions of spottail shiners (*Notropis hudsonius*), yellow perch (*Perca flavescens*), and northern pike (*Esox lucius*). J. Fish. Res. Board Can. **30**: 1161–1178.

Pihl, L. 1982. Food intake of young cod and flounder in a shallow bay on the Swedish west coast. Neth. J. Sea. Res. **15**: 419–432.

Riley, J.D., and Parnell, W.G. 1984. The distribution of young cod. *In* The propagation of cod, *Gadus morhua* L. *Edited by* E. Dahl, D.S. Danielssen, E. Moksness, and P. Solemdal. Flød. Rapp. **1**: 563–580. (ISSN 0333–2594.)

Robb, A.P. 1981. Observations on the food and diel feeding behaviour of pelagic 0-group gadoids in the northern North Sea. J. Fish Biol. **18**: 183–194.

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Siegel, S. 1956. Nonparametric statistics for the behavioural sciences. McGraw-Hill, New York.

Taggart, C.T., Anderson, J., Bishop, C., Colbourne, E., Hutchings, J., Lilly, G., Morgan, J., Murphy, E., Myers, R., Rose, G., and Shelton, P. 1994. Overview of cod stocks, biology, and environment in the northwest Atlantic region of Newfoundland, with emphasis on northern cod. ICES Mar. Sci. Symp. **198**: 140–157.

Tupper, M., and Boutilier, R.G. 1995. Effects of habitat on settlement, growth, and postsettlement survival of Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **52**: 1834–1841.

Tveite, S. 1984. 0-Group cod investigations on the Norwegian Skagerrak coast. *In* The propagation of cod, *Gadus morhua* L. *Edited by* E. Dahl, D.S. Danielssen, E. Moksness, and P. Solemdal. Flød. Rapp. **1**: 581–590. (ISSN 0333–2594.)

Tyler, A.V. 1970. Rates of gastric emptying in young cod. J. Fish. Res. Board Can. **27**: 1177–1189.

Webster, D.A. 1942. Food progression in young white perch *Morone americana* (Gmelin) from Bantam Lake, Connecticut. Trans. Am. Fish. Soc. **72**: 136–144.

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Nearshore settlement and localized populations of age 0 Atlantic cod (*Gadus morhua*) in shallow coastal waters of Newfoundland

Scott M. Grant and Joseph A. Brown

Abstract: Mark–recapture experiments and seasonal sampling were carried out to examine the nearshore movements, abundance, and behaviour patterns of age 0 Atlantic cod (*Gadus morhua*) in eelgrass (*Zostera marina*) and no-eelgrass habitat in Trinity Bay, Newfoundland, during 1994 and 1995. Cod remained localized, not moving further than a few hundred metres in eelgrass and no-eelgrass habitats for several weeks after settling from a pelagic habit, and may remain localized during their first winter. Observations from this study of bulk movements of marked and unmarked cod, high within-site variation in catch rates during the day, and significant day–night differences in the mean and variance of catch data, combined with results from related studies, provide indirect evidence that age 0 cod shoal during the day and disperse at night within the study area. Behaviour patterns exhibited by age 0 cod (restricted nearshore movements, diurnal shoaling, and preference for structurally complex habitat) are mechanisms for predator avoidance, suggesting that predation risk is high in coastal Newfoundland. A significant increase in abundance of age 0 cod in less suitable habitat (no-eelgrass cover) when settlement strength was high is consistent with the hypothesis of density-dependent habitat selection.

Résumé : Des essais par marquage–recapture et des échantillonnages saisonniers ont été réalisés afin d'examiner les déplacements littoraux, l'abondance et le comportement des morues de l'Atlantique (*Gadus morhua*) d'âge 0 dans des habitats à zostère (*Zostera marina*) ou sans zostère de la baie Trinity, à Terre-Neuve, en 1994 et 1995. Les morues sont demeurées au même endroit, se déplaçant d'au plus quelques centaines de mètres dans les deux types d'habitat pendant plusieurs semaines après s'être fixées, après leur période pélagique, et pouvaient y passer leur premier hiver. Les observations faites des déplacements généraux des morues marquées et non marquées, la forte variation locale des taux de capture pendant le jour et les écarts importants entre le jour et la nuit de la moyenne et de la variance des données sur les prises, qui s'ajoutent aux résultats d'études connexes, constituent des preuves indirectes de la formation de bancs par les morues d'âge 0 pendant le jour et de leur dispersion pendant la nuit, dans la zone étudiée. Les régimes comportementaux des morues d'âge 0 (déplacements littoraux limités, formation de bancs le jour et préférence pour les habitats à structure complexe) constituent des mécanismes d'évitement des prédateurs et cela porte à croire que les risques de prédation sont élevés dans les eaux côtières de Terre-Neuve. Une augmentation appréciable de l'abondance des morues d'âge 0 dans un habitat moins approprié (absence de zostère formant couvert) au moment où beaucoup de morues cessent d'être pélagiques est cohérente avec l'hypothèse du choix de l'habitat en fonction de la densité.
[Traduit par la Rédaction]

Introduction

It is well established that trade-offs between food availability and predation risk influence fish distribution and activity; alterations in behaviour may occur at various life history stages and reflect a balance between food intake and the need to be vigilant (Lima and Dill 1990). Helfman (1986) reviewed the diel behaviour of fish, noting that "many fish appear to separate the day into an active, food gathering phase and a relatively inactive, resting phase that is ultimately linked to predator avoidance." For example, on coral reefs, where predation risk is high, small zooplanktivorous fish generally feed over refuge sites during the day as parts of large relatively stationary aggregations and seek cover during increased activity of nocturnal fish (Helfman 1986). Diel behaviour patterns are well established for fish inhabiting coral reefs. However, Helfman (1986) suggested that convergent patterns in fundamental activities can be expected in almost any fish assemblage; behaviour patterns that successfully reduce predation risk while maintaining adequate food intake may transcend geographic and taxonomic boundaries.

Coastal settlement of age 0 Atlantic cod (*Gadus morhua*) may result in movement into regions occupied by older conspecifics, and cannibalism is common when large and small cod occur together (Bogstad et al.1994). Age 0 cod appear to reduce encounter rates with larger conspecifics by settling in shallower waters that exhibit protective bottom cover (Riley and Parnell 1984; Gotceitas et al. 1997; Grant and Brown 1998). However, larger nocturnally active conspecifics may enter shallow coastal waters at night (Pihl 1982; Clark and Green 1990; Keats 1990; Grant and Brown 1998), and as potential prey, age 0 cod appear to assess this increased predation risk by adjusting their behaviour. For example, although age 0 cod of similar size were zooplanktivorous during both the pelagic (Robb 1981) and nearshore demersal phase (Olsen and

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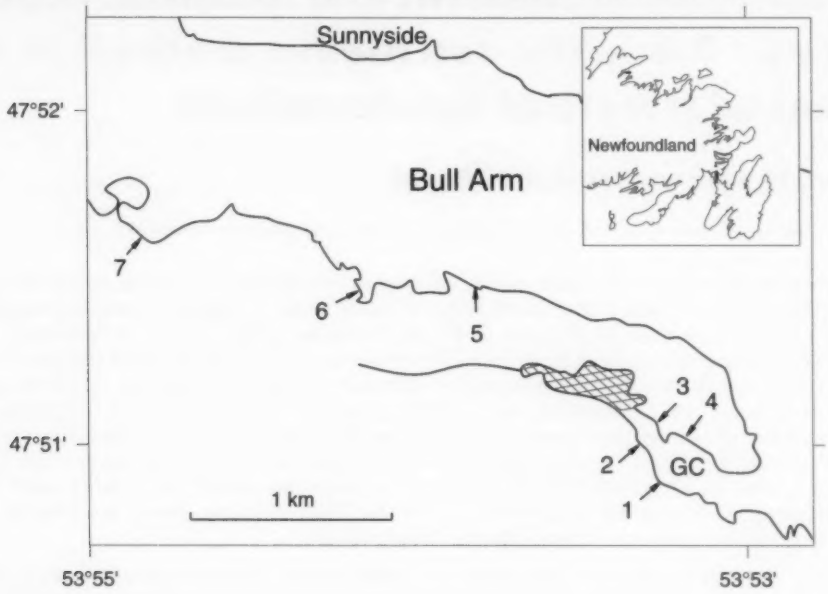
Fig. 1. Study area in Bull Arm of Trinity Bay, Newfoundland, indicating study site locations. GC, Goose Cove.



Soldal 1989; Grant and Brown 1998), they exhibited contrasting nocturnal and diurnal activity cycles, respectively, whereas cod that settle in offshore waters still maintain a nocturnal activity cycle (Lough et al. 1989). Echosounder studies in Norway document a diurnal activity cycle and schooling behaviour by age 0 cod in coastal environments (Olsen and Soldal 1989), and a diurnal activity cycle has also been reported for nearshore concentrations of zooplanktivorous age 0 cod in coastal Newfoundland (Grant and Brown 1998). Individual fish that join a school or shoal may locate patchy food faster (i.e., zooplankton), devote less time to vigilant behaviour, and forage longer (Pitcher 1986). Site fidelity and crypsis in structurally complex habitats may also reduce predation risk (Lough et al. 1989; Tupper and Boutilier 1995*b*); however, the cited literature suggests that behaviour patterns of coastal populations of age 0 cod may also converge on those observed for zooplanktivorous fish on coral reefs.

Laboratory and field studies provide evidence that the distribution and survival of small juvenile cod are dependent on habitat type (Lough et al. 1989; Tupper and Boutilier 1995*b*; Gotceitas et al. 1997) and shoaling near protective bottom cover provides a means of evading predators (Pitcher 1986). Eelgrass (*Zostera marina*) habitat appears to influence the distribution of small juvenile cod in coastal waters throughout the North Atlantic (Støttrup et al. 1994; Tupper and Boutilier 1995*b*), and a recent study on habitat use of age 0 cod in coastal Newfoundland has provided evidence of an almost exclusive use of eelgrass (Gotceitas et al. 1997). If fish actively select habitats due to differing levels of density-dependent resources such as food and shelter, then as density increases and habitat suitability declines, distribution should expand to include the use of previously less suitable habitats (MacCall 1990). Density-dependent habitat selection has been used to explain positive correlations between abundance and area occupied by large juvenile and adult cod (Swain 1993); however, the importance of settlement strength to the distribution of age 0 cod in coastal areas has only recently been considered (Schneider et al. 1997).

Our current understanding of the distribution, movement, and behaviour of age 0 cod in coastal Newfoundland is limited to underwater observations and capture studies that can only describe occurrence or absence at specific sites at one moment in time. Consequently, these studies cannot distinguish between small- or large-scale movements and tell us little about the mechanisms that influence distribution and behaviour in space and time. Recent evidence suggests that day–night differences in behaviour of age 0 cod may be related to varying levels of predation risk (Grant and Brown 1998), and studies indicate that predation risk and movement rates of animals vary inversely (Perry and Pianka 1997). In this study, we used mark–recapture experiments to determine whether postsettled age 0 cod exhibit fidelity at two nearshore locations that differ in habitat type (eelgrass versus no eelgrass) in Trinity Bay, Newfoundland, during the autumns of 1994 and 1995. Standardized catches were also used to determine seasonal and diel behaviours. These juveniles are an inshore component of the North Atlantic cod stock which has been under moratorium since 1992 (Taggart et al. 1994). Anticipating year-to-year variation in abundance of the 0-group cohort, we also tested the hypothesis of density-dependent habitat selection within the study area.

Materials and methods

Study area

A description of the nearshore movements of age 0 cod was obtained from mark–recapture experiments and seasonal sampling carried out at Goose Cove (sites 1–4; 47°51′N, 53°54′W) and across from the community of Sunnyside (sites 5–7; 47°51′N, 53°55′W) (Fig. 1).

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Both study areas are located in Bull Arm of Trinity Bay, Newfoundland.

The shoreline of Bull Arm is typical of the northeast coast of Newfoundland, consisting largely of steep cut banks with narrow beach areas, where present. Bull Arm is protected from the open ocean and has a tidal amplitude of about 1.2 m. The nearshore zone at the Sunnyside study location is dominated by a relatively flat and gradual sloping bottom. Bottom depth in the nearshore zone increases gradually to 10–15 m, forming a ledge that extends about 100 m from shore, at which point the depth increases sharply (>50 m). Substrate type within the 15-m depth zone largely consisted of sand–gravel–cobble and sparse patches of vegetation.

Goose Cove is a shallow, well-protected cove. Differences in overall depth allow a separation of the cove into two distinct regions. The first region is located at the head of the cove (cross-hatched area, Fig. 1) where the maximum low-tide depth is about 0.7 m. The bottom consists of sand and silt deposited by a stream entering from the east. Cod were not observed in this region during the day. The remainder of the cove forms a large basin that can be separated into two distinct habitat types. A substrate of mainly sand–gravel extends to a distance of 30–60 m out from shore, and eelgrass is distributed throughout this zone to a depth of about 5.0 m. The substrate in the central region of the cove consists of sand, silt, and mud.

All sample sites were standardized to cover a bottom area of about 800 m^2 (16 × 50 m). In Goose Cove, low-tide depth at 50 m from shore was 3.0–8.0 m and eelgrass cover was 25–75% for sites 1–4 (Fig. 1). The maximum low-tide depth 50 m from shore at the Sunnyside sampling sites was 3.0–8.5 m (Fig. 1). There was no vegetative cover at site 5, macroalgae cover at site 6 was low (<5%), and site 7 had about 5% eelgrass cover.

Juvenile cod sampling

A beach seine with headrope and footrope lengths of 24.4 and 26.2 m, respectively, was used to collect cod. The seine was made from a knotless nylon netting with a stretched mesh size of 19 mm in the wings and belly and 13 mm in the codend, and a 1.5-m length of 9-mm mesh was attached to the codend. A 55-m towrope was attached to each wing.

The net was deployed from a small boat (6 m) at a distance of 50 m from shore and then retrieved at a constant and even rate by two individuals standing 16 m apart on the shore. During each set, the towropes were located in the same location onshore, thereby keeping the area sampled at each site fairly constant. The seine sampled the water column from the substrate to 2 m off the bottom. Fish were placed in a large tub filled with seawater and sorted by age-class. SCUBA observations (Gotceitas et al. 1997) have shown that 95% of the fish in the path of this net are captured.

Nearshore studies on the northeast coast of Newfoundland indicate that there are two or three temporally spaced influxes of recently settled cod (Methven and Bajdik 1994; Grant and Brown 1998). Hatch dates and egg development times indicate that the first settlement pulse, occurring in August–September, coincides with peak spawning for Trinity Bay and later autumnal settlement pulses are also likely to have been spawned in Trinity Bay (Pinsent and Methven 1997). Recently settled cod typically lose their pelagic pigmentation within 1–2 weeks postsettlement (Tupper and Boutilier 1995*a*). In the current study, recently settled cod (3.8–6.5 cm) were distinguished by a barred or checkerboard pigmentation pattern on a pale background and a silvery underbelly. Postsettled juveniles (>5.0–7.0 cm) are mottled and heavily pigmented with a white underbelly and can also be identified by the presence of encysted metacercaria of the digenean *Cryptocotyle lingua*. This classification system exhibits overlap in body size resulting from high variation in size at settlement.

Mark–recapture experiments

Age 0 cod were sampled and enumerated weekly at four sites in Goose Cove from September to December in 1994 and 1995 (sites 1–4, Fig. 1). Two mark–recapture experiments were conducted during 1994. The first experiment began on September 24 when 667 postsettled age 0 cod were marked by clipping the dorsal and ventral lobes of the caudal fin. A second experiment was initiated on November 13 when 654 postsettled age 0 cod were marked by clipping the dorsal lobe of the caudal fin. Both marking programs were conducted on cod from the August–September settlement pulse (see Results) and were restricted to cod captured at a single site (site 2, Fig. 1). Once captured, cod were held in 150-L tanks that allowed a free flow of seawater. Cod were marked, placed in recovery tanks, and monitored for at least 1 h before being released at site 2.

A single mark–recapture experiment was conducted in Goose Cove during 1995. A total of 1188 age 0 cod from the August–September settlement were marked on September 16 by clipping the dorsal lobe of the caudal fin. This marking program was similar to that outlined for 1994.

At Sunnyside, a single mark–recapture experiment was conducted on cod from the August–September settlement in 1994. This area was identified as a suitable sampling location on October 22, at which time, 624 age 0 cod were marked at site 6 (Fig. 1) by clipping the ventral lobe of the caudal fin. Pre- and post-marking procedures were similar to those for the Goose Cove experiments. In 1995, there were too few age 0 cod captured at Sunnyside to conduct mark–recapture experiments.

Limited beach access required a modification of the sampling design at Sunnyside. Cod were sampled at site 6 for 8 consecutive weeks (October 22 to December 10) during 1994. Each weekly sampling program consisted of five consecutive hauls at site 6. Cod collected during each haul were held in separate 150-L tanks until all hauls were completed (about 2 h). Cod were counted and then released. Secondary sample sites (sites 5 and 7) were sampled approximately fortnightly (i.e., October 30, November 13, November 26, and December 10) in 1994.

In 1995, all Sunnyside sites were sampled from September to December. Sampling at site 6 was similar to that in 1994, and sites 5 and 7 were sampled throughout the season.

Data obtained during the mark–recapture experiments were used to estimate the population size of cod from the August–September settlement pulse for Goose Cove and the Sunnyside study area. Population size was estimated using the simple Petersen formula (Ricker 1975) which states $N = MC/R$ where N is the estimate of population size, M is the number of marked fish in the population, C is the total number of fish in the recapture sample, and R is the number of marked fish recaptured in the sample. Biases associated with estimates of N are negligible when MC exceeds $4N$ or if R is at least 7 (Robson and Regier 1964). These criteria were met during our mark–recapture experiments. Differential mortality and immigration may also bias estimates of N. In an attempt to eliminate these factors, N was estimated 6–8 days after the initial release of marked fish.

Fifty age 0 cod were randomly removed from the weekly catches at site 2 in 1994 and 1995 and at site 6 in 1994. These samples included both recently settled and postsettled cod. When present in high numbers, an additional sample of up to 25 recently settled cod was also collected. Cod were killed (MS 222), frozen (dry ice), and later thawed for measurement of standard length (SL, ± 1.0 mm).

Additional sampling

A diel survey was conducted at site 2 during 1994 to determine (*i*) whether marked individuals remain within the study area at night and (*ii*) day–night differences in the catch of age 0 and age 1 cod. Samples were conducted at 3-h intervals over a 24-h period in September and October. Day–night differences in the mean catch of age 0 and age 1 cod were assessed using a randomization test (Siegel 1956). A two-tailed variance ratio test (Zar 1984) was used to compare variation between day and night catches of age 0 cod. Day–night variation in catch was also assessed from diel capture rate data collected at site 2 in the previous year (Grant and Brown 1998).

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Table 1. Total beach seine catches (n) of age 0 Atlantic cod and percentage of recently settled cod (%RS) at Goose Cove (sites 1–4) and Sunnyside (sites 5–7), Newfoundland, from September to December 1994 and 1995.

	Goose Cove		Sunnyside			Goose Cove		Sunnyside	
1994	n	%RS	n	%RS	1995	n	%RS	n	%RS
Sept. 16	381	33.1	—	—	Sept. 16	251	8.4	11	0
Sept. 24	779	3.9	—	—	Sept. 24	194	4.6	10	10.0
Sept. 30	890	1.1	—	—	Sept. 30	465	48.0	2	0
Oct. 8	1001	8.9	—	—	Oct. 6	442	31.0	0	0
Oct. 15	1206	21.4	—	—	Oct. 14	356	23.0	6	0
Oct. 22	780	4.2	716	5.9	Oct. 22	366	12.3	18	11.0
Oct. 30	789	2.5	165	18.2	Oct. 28	357	4.5	4	0
Nov. 5	716	1.3	257	3.1	Nov. 12	336	0	11	0
Nov. 13	721	0.5	114	0.9	Nov. 26	522	40.0	2	0
Nov. 19	361	0	56	0	Dec. 10	490	35.3	33	12.1
Nov. 26	545	6.4	477	1.5					
Dec. 3	680	2.6	415	5.3					
Dec. 10	718	2.4	102	1.0					

Note: —, no data.

Winter sampling was conducted to determine if marked cod were present at the study sites. Both study locations were resampled on February 19 and March 26, 1995.

Results

Autumnal influxes of recently settled cod

A total of 9522 and 3779 age 0 cod were captured in Goose Cove during autumn of 1994 and 1995, respectively (Table 1). There were three temporally spaced influxes of recently settled cod in Goose Cove during 1994 and 1995 (Table 1; Fig. 2). In both years, the first settlement pulse began before sampling commenced. During 1994, recently settled cod represented the highest proportion of the total catch (sites 1–4 combined) on September 16. The decrease in percentage of recently settled cod on September 24 indicates that the first settlement pulse was largely complete by this time. The second settlement pulse occurred in mid-October and coincided with the seasonal peak in total catch in 1994 (Table 1). Apparently, the first two settlement pulses were about 2 weeks earlier in 1995. When sampling began in September 1995, the proportion of recently settled cod from the first settlement was considerably lower than that observed on the same day in 1994 and the proportion of recently settle cod from the second pulse peaked 2 weeks earlier (September 30) in 1995 (Table 1). The late autumn influx was similar in both years (i.e., late November, Table 1).

Length–frequency distributions for cod sampled in Goose Cove indicate a clear size separation between cod from the August–September and October settlement pulses in 1994 and 1995 (Fig. 2). By mid-October 1994, the proportion of recently settled cod declined abruptly (Table 1). Length–frequency distributions after the decline indicate that juveniles from the August–September settlement dominated in Goose Cove. During 1994, smaller juveniles from the October settlement were not well represented again until late November (Fig. 2). In contrast, cod from the October settlement pulse were well represented in the length–frequency distributions throughout the autumn of 1995, a year of seasonally lower total catch rates (Table 1) and lower absolute abundance (N) of cod from the August–September settlement pulse (see mark–recapture experiments). The November settlement pulse resulted in a clear trimodal length distribution in 1994 and 1995 (Fig. 2).

A total of 2302 age 0 cod were captured at Sunnyside from October to December 1994 (Table 1). Most of these cod were captured at site 6 (92.2%). Length–frequency distributions at Sunnyside (Fig. 3) were similar to those observed in Goose Cove (Fig. 2), indicating that all three settlement pulses were widespread in Bull Arm in 1994. Biomodal length distributions in October–November contrasted the length distributions for Goose Cove (Figs. 2 and 3), indicating that cod from the October settlement were well represented at Sunnyside in 1994.

The seasonal catch of age 0 cod was considerably lower at Sunnyside in 1995 (Table 1). The highest catches were in eelgrass at site 7 where most of the cod were captured (79.4%).

Mark–recapture experiments

Marked cod from the August–September settlement pulse were recaptured in Goose Cove over a 12-week period in 1994 and 1995 (Fig. 4). Cod marked in Goose Cove were not recaptured at Sunnyside in 1994 or 1995 and cod marked at Sunnyside were not recaptured in Goose Cove. Thus, there was no evidence of migration between study locations.

The weekly catch of postsettled cod at each site within Goose Cove was expressed as a percentage of the total catch of postsettled cod in the combined samples from sites 1–4 in 1994 (Fig. 5*a*) and 1995 (Fig. 5*c*), and the number of marked cod recaptured at each site was expressed as a percentage of the total number of marked cod recaptured at sites 1–4 in 1994 (Fig. 5*b*) and 1995 (Fig. 5*d*). Comparable weekly shifts in distribution of marked and unmarked cod and the recapture of marked cod at all sample sites in 1994 and 1995 indicate random mixing and bulk movement between sites. Sites 1 and 3 had relatively low eelgrass cover (25 and 30%, respectively) and seemed to represent peripherally used regions supporting a small proportion of the total weekly catch in both years (14.3–32.3% in 1994 and 7.9–23.3% in 1995). Cod appeared to be more highly concentrated in the vicinity of sites that exhibited the highest eelgrass cover (i.e., 75% at site 2 and

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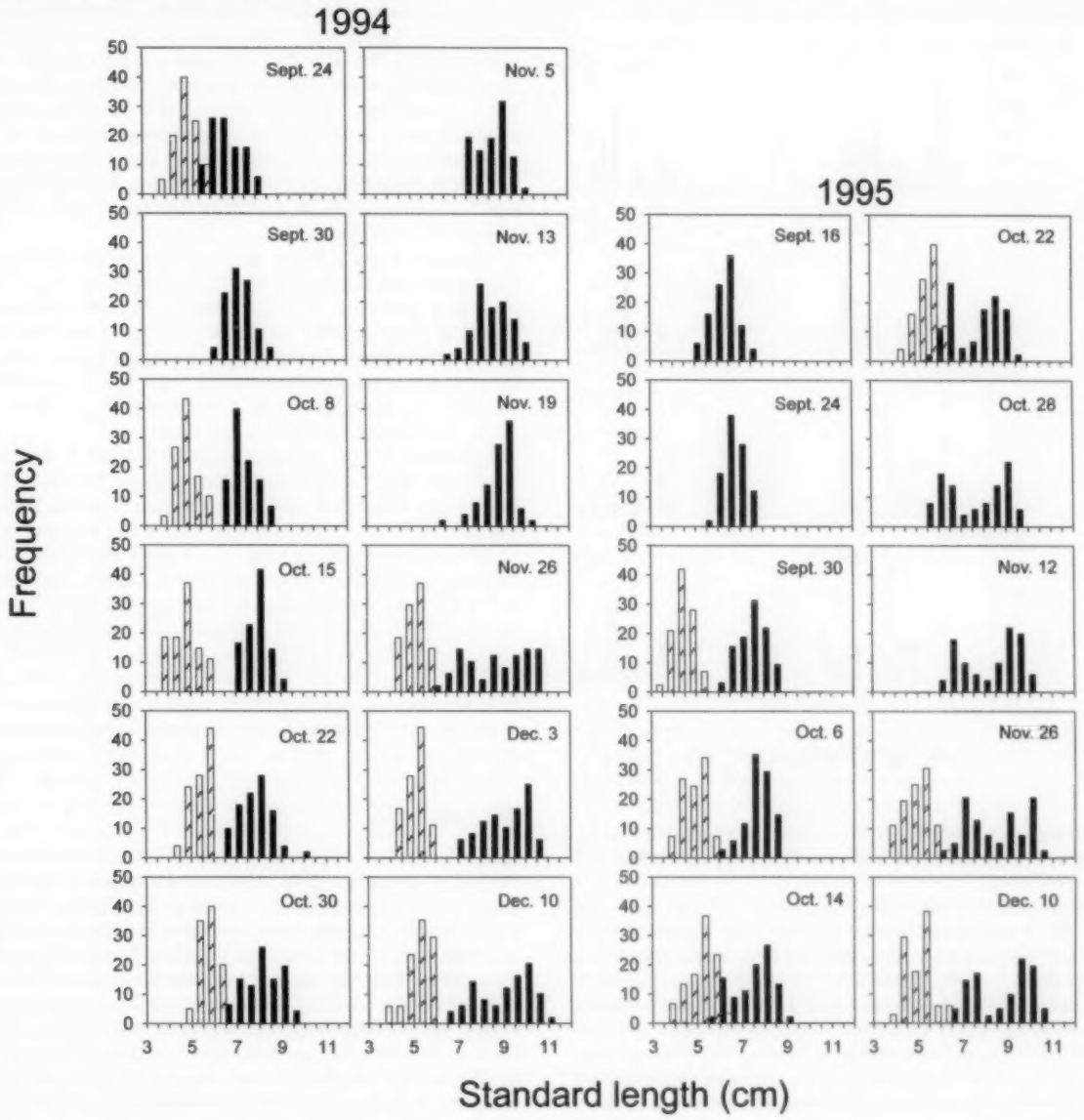
Fig. 2. Length–frequency distributions for each of recently settled (hatched bars) and postsettled (solid bars) age 0 Atlantic cod in Goose Cove, Newfoundland, September–December 1994 and 1995.



65% at site 4) and distribution between these sites changed in a converse manner in both years (Fig. 5). A plot of catch against cumulative catch at site 2 during the 1995 marking program, which was conducted over a 4-h period, illustrates that bulk movements occurred throughout the day (Fig. 6).

One age 0 cod (unmarked) was captured at site 5 (Sunnyside) in 1994. Age 0 cod were captured at site 7 during all of the fortnightly collections (four cod on October 30, 62 cod on November 13, 17 cod on November 26, and 95 cod on December 10). Cod were captured at site 6 throughout the Sunnyside mark–recapture experiment (Table 2). There was high temporal variation in the catch at site 6 at the scale of hours (hauls 1–5) and weeks, a result comparable with that observed for site 2.

Two cod previously marked at site 6 were recaptured at site 7 on November 13, and one marked cod was recaptured on December 10. Marked cod were recaptured at site 6 over a period of 7 weeks (Table 2). The percent recapture of marked cod, averaged over all five hauls at site 6, showed little change from October 30 to November 5, 1994 (Table 2); however, the total catch of postsettled cod almost doubled over the same period. Marked cod were recaptured in all five hauls on October 30, November 5, and November 26, and two seasonal peaks in the total catch (November 5 and 26) coincided with

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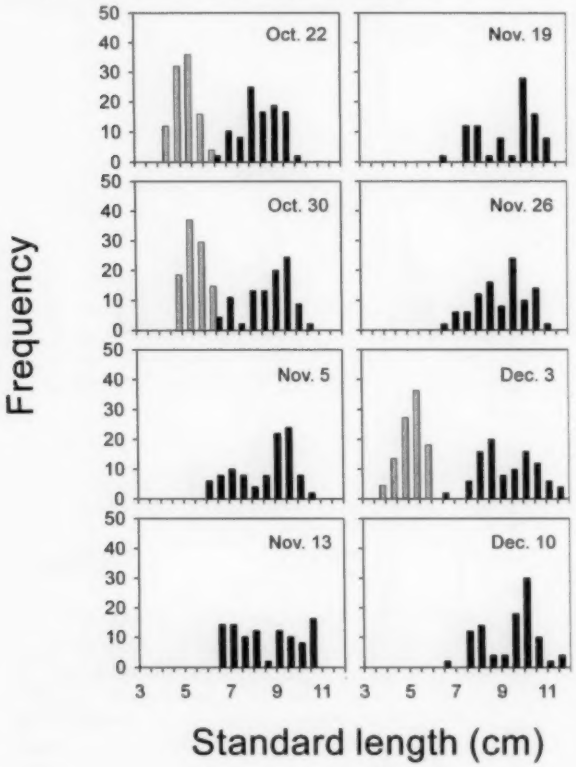
Fig. 3. Length–frequency distributions for each of recently settled (hatched bars) and postsettled (solid bars) age 0 Atlantic cod at Sunnyside, Newfoundland, October–December 1994.



peaks in the total number of marked cod recaptured (Table 2). Overall, these results indicate random mixing of marked and unmarked cod.

Mark–recapture abundance estimates indicate that cod from the August–September settlement were 4.9 times more abundant in Goose Cove in September 1994 than in September 1995 (Table 3). This difference was significant, as the 95% CI's did not overlap between years. Bias associated with immigration was likely minimal, as cod were marked after the first influx in both years (Table 2). During 1994, the number of cod from the August–September settlement declined by 50% in Goose Cove by mid-November; however, cod from this settlement were significantly more abundant in Goose Cove than at Sunnyside, as the 95% CI's did not overlap between locations in 1994 (Table 3).

Year-to-year differences in seasonal mean density were also apparent at the study locations. Relative indices of abundance (catch per unit area, sites 1–4), calculated as the seasonal mean (± 95% CI) of recently settled and postsettled cod, were 2.1 times higher in 1994 (0.230 ± 0.039) compared with 1995 (0.112 ± 0.020). Fish per unit area of habitat sampled at Sunnyside from October 22 to December 10 were 32 times higher in 1994 (0.064 ± 0.040) than in 1995 (0.002 ± 0.002). Year-to-year differences in mean density of age 0 cod in the nearshore environment of Bull Arm were apparently related to the strength of the August–September settlement pulse.

Additional sampling

Marked age 0 cod were recaptured throughout the diel period, indicating that they occupy the same general areas at night that they occupy during the day. The catch of age 0 cod was always higher during the day, declined after sunset, remained low throughout the night, and then increased sharply at dawn (Table 4). Conversely, the catch of age 1 cod increased at night. Randomization tests revealed a significant difference in the mean catch between light periods for age 0 cod (September 24: $p = 0.008$; September 30: $p = 0.016$; October 8: $p = 0.016$) and age 1 cod (September 24: $p = 0.008$; September 30: $p = 0.008$; October 8: $p = 0.008$).

Variance in the catch of age 0 cod was higher during the day on all dates sampled in 1994 (September 24: $F_{4,3} = 18.8$, $p = 0.018$; September 30: $F_{4,3} = 264.8$, $p << 0.001$; October 8: $F_{4,2} = 250.1$, $p = 0.004$). Similarly, analysis of our 1993 data (Table 1; Grant and Brown 1998), revealed a higher variance in catch during the day (September: $F_{4,3} = 193.5$, $p << 0.001$; October: $F_{2,3} = 17.2$, $p = 0.023$; November: $F_{4,3} = 50.5$, $p = 0.004$; December: $F_{3,2} = 262.8$, $p = 0.004$).

Landward ice precluded collections at sites 1–4 (Goose Cove) and sites 5 and 6 (Sunnyside) during February 1995. Fifteen age 1 and five age 2 cod (formerly age 0 and age 1, respectively) were captured at site 7 at a water temperature of –1.2°C. In March 1995, a total of 131 age 1 and 12 age 2 cod were captured at site 4 in Goose Cove at a water temperature of 0.5°C. The length–frequency distribution of age 1 cod was trimodal (Fig. 7) and similar to that observed on December 10, 1994 (Fig. 2). Eight (6.1%) of the age 1 cod captured in March were initially marked at site 2 on November 13, 1994. The length–frequency distribution of marked cod indicates that these fish were from the August–September settlement pulse (Fig. 7).

Discussion

In the current study, age 0 cod remained localized, not moving more than a few hundred metres within shallow nearshore habitats for several weeks after settling. Recapture of marked cod in March suggests that juveniles may remain localized over their first winter, as in Loch Torridon, Scotland (Hawkins et al. 1985). Bulk movements of marked and unmarked cod, high within-site variation in catch at the scale of hours and weeks, and day–night differences in mean and variance of the catch data provide indirect evidence of diurnal shoaling activity. Given that variance of catch data is typically positively correlated with the mean, a higher variation in catch would be expected in the daytime, when the larger catches were made. However, the true mean should be the same between light periods, as sampling was conducted on the same population. Day–night patterns in the mean and variation of catch data did not differ seasonally or between years (Grant and Brown 1998). Given that marked age 0 cod were generally recaptured in similar proportions during both light periods, we interpret these day–night patterns in catch rates to reflect a local dispersal by shoals at night. These day–night differences in shoaling are consistent with findings on age 0 cod in the nearshore regions of Norway (Olsen and Soldal 1989).

Inferences on shoaling within the study area are also supported by recent documentation of zooplanktivory and a strict diurnal foraging cycle by age 0 cod, which appears to be

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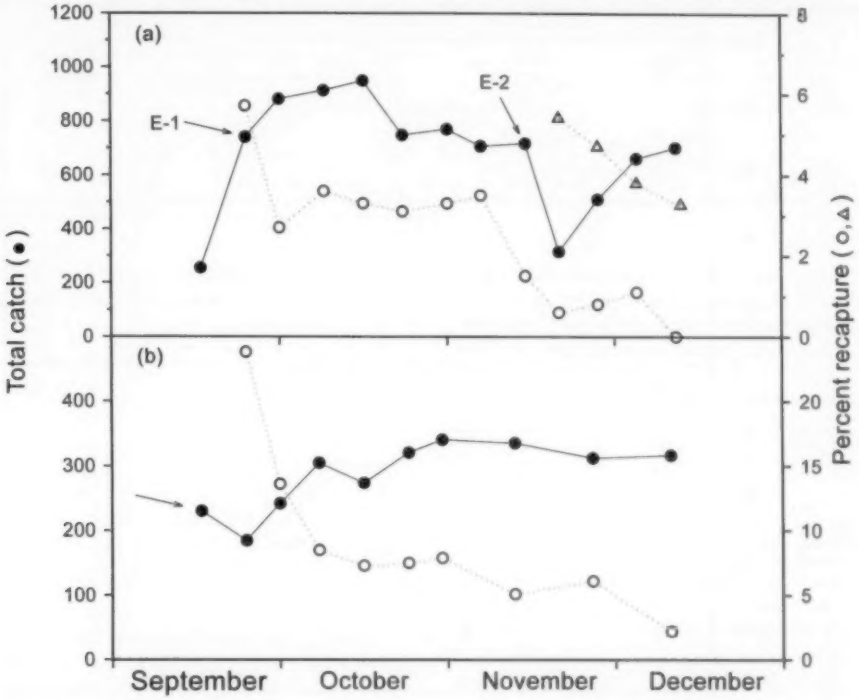
Fig. 4. Total catch of postsettled age 0 Atlantic cod and percent recapture of cod marked on (*a*) September 24 (E-1; open circles) and November 13 (E-2; open triangles), 1994, and (*b*) September 16, 1995 (arrow; open circles) in Goose Cove, Newfoundland.



related to increased foraging activity and abundance of older conspecifics in shallow waters at night (Grant and Brown 1998). Options that fish have to reduce the threat of predation while foraging appear to be limited to inhabiting areas of low predator abundance or forming schools or shoals. Information about the approach of a predator is transferred across a foraging shoal (Magurran and Higham 1988), and laboratory investigations on predation risk in cod collected in the nearshore environment of Newfoundland (Gotceitas and Brown 1993) reported the formation of loose groups of age 0 cod up in the water column in the absence of a predator and subsequent movement out of the water column when a predator (older conspecific) was introduced. Although age 0 and age 1 cod are commonly captured in the same habitat during the day (Gotceitas et al. 1997; Grant and Brown 1998; this study), studies suggest a shoreward movement by age 1 and older conspecifics (ages 2–3) at night (Pihl 1982; Clark and Green 1990; Keats 1990). Given that intercohort cannibalism has been documented for 1- to 3-year-old cod in the wild (Bogstad et al. 1994; Grant and Brown 1998), we suggest that age 0 cod shoal in the study area during the day to enhance foraging success and increase detection of age 1 cod and then disperse and cease foraging at night due to increased shoreward movement of 1- to 3-year-old conspecifics. Studies show that shoaling may provide protection from small predators but provides less protection when larger predators are present (Pitcher 1986).

Beach seine and bottom trawl surveys in coastal Newfoundland document increased catch of age 0 cod at night (Methven and Bajdik 1994; Methven and Schneider 1998), a result that we interpret to be consistent with a nocturnal dispersal of this age-class. Prerecruit beach seine and bottom trawl surveys, based on blind random spot samples, are more likely to capture fish that are sparsely distributed, such that localized, yet mobile concentrations of age 0 cod may largely go undetected during the day. If the distribution of age 0 cod in the nearshore environment is currently centred at depths of 4–7 m (Methven and Schneider 1998), than collections taken at very shallow-water sampling sites (1.2 m, Methven and Bajdik 1994) may not be representative of the typical daytime densities in the nearshore. However, increased abundance of age 0 cod in very shallow water at night is consistent with a dispersal in response to increased predation risk by shoreward-migrating older conspecifics (Pihl 1982; Clark and Green 1990; Keats 1990; Grant and Brown 1998).

Although based on small temporal and spatial scales, our results on variation in settlement strength and the distribution and abundance of age 0 cod in eelgrass and no-eelgrass habitat are consistent with the hypothesis of density-dependent habitat selection (but see Schneider et al. 1997). Studies on cod populations in the Gulf of St. Lawrence and east of Newfoundland (Swain and Wade 1993; Taggart et al. 1994) also provide evidence of density-dependent distributions. In this study, the presence of eelgrass was an important factor influencing the nearshore distribution of age 0 cod, a result that is consistent with findings in coastal waters throughout the North Atlantic (Støttrup et al. 1994; Tupper and Boutilier 1995*a*, 1995*b*; Gotceitas et al. 1997). High settlement in eelgrass in years of high and low abundance is consistent with the hypothesis that the most suitable habitats are generally always fully utilized

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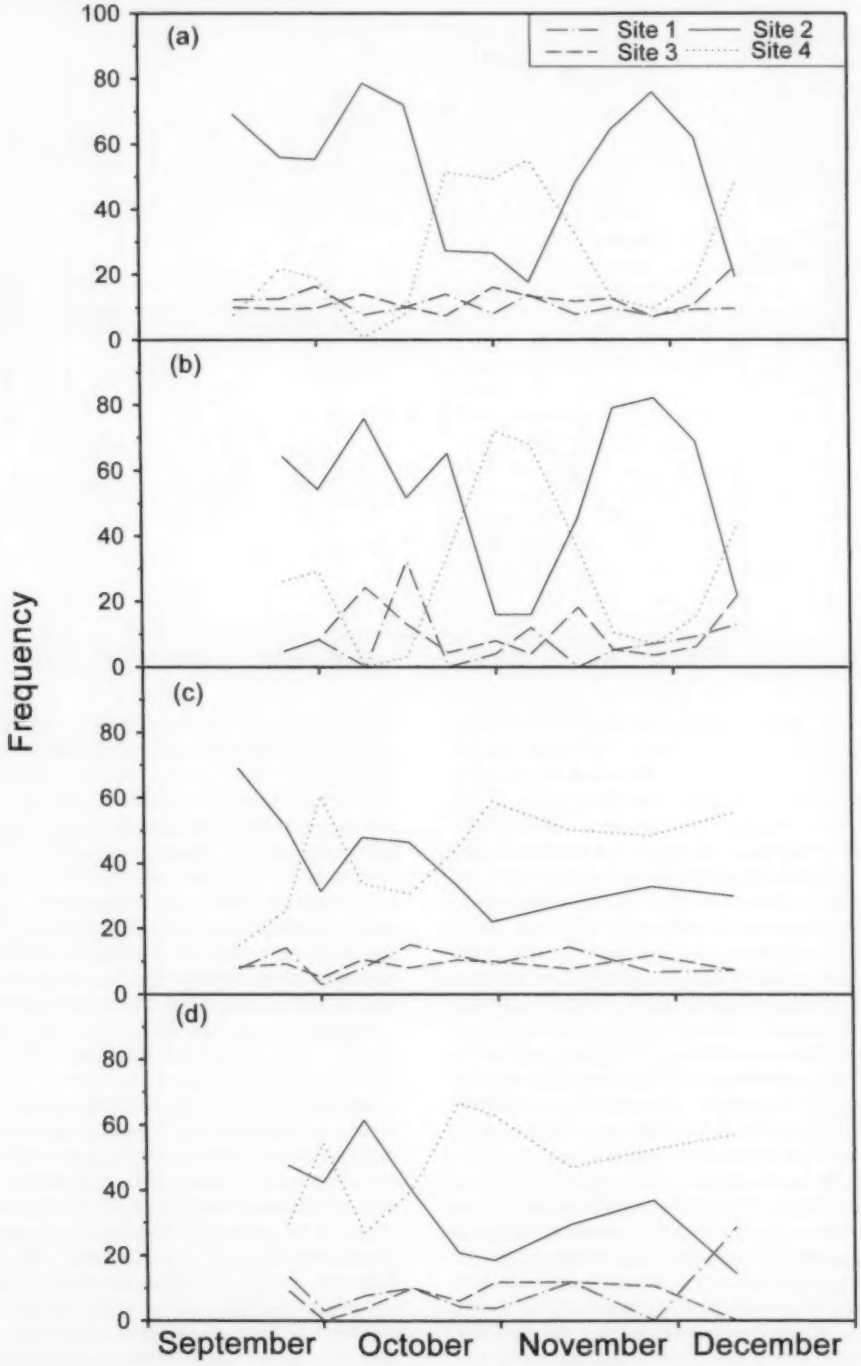
Fig. 5. Seasonal variation at sites 1–4 in Goose Cove, Newfoundland, in the distribution of postsettled age 0 Atlantic cod during (*a*) 1994 and (*c*) 1995 and of marked cod during (*b*) 1994 and (*d*) 1995. Values are expressed as a percentage of the total number of postsettled cod captured and of the total number of marked cod recaptured at all sites.



regardless of year-class strength (Olsen and Soldal 1989). Year-to-year variation in abundance in no-eelgrass habitat suggests that this habitat is less suitable, only supporting high densities of age 0 cod when more suitable nearby habitats are fully utilized.

In this study, the first autumnal settlement pulse appeared

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Table 2. Beach seine catches (number per haul) of postsettled age 0 Atlantic cod during five consecutive hauls at site 6 (see Fig. 1) at Sunnyside, Newfoundland, from October to December 1994.

Sample	October 22	October 30	November 5	November 13	November 19	November 26	December 3	December 10
1	181 (—)	27 (22.2)	66 (30.3)	7 (28.6)	2 (0)	14 (7.1)	26 (3.8)	1 (0)
2	327 (—)	6 (16.6)	24 (12.5)	1 (0)	38 (7.9)	127 (9.4)	3 (0)	3 (33.3)
3	24 (—)	17 (23.5)	11 (27.3)	34 (11.8)	0 (0)	17 (5.9)	325 (5.2)	1 (0)
4	70 (—)	79 (21.5)	98 (23.5)	9 (22.2)	14 (14.3)	164 (6.1)	14 (7.1)	0 (0)
5	114 (—)	5 (20.0)	50 (10.0)	0 (0)	2 (0)	131 (6.1)	15 (6.7)	2 (0)
Total catch	716	134 (21.6)	249 (21.7)	51 (15.7)	56 (8.9)	453 (7.1)	393 (5.1)	7 (14.3)

Note: Values in parentheses are percentages in catch of marked cod. —, no data.

Fig. 6. Catch versus cumulative catch for age 0 cod sampled over a 4-h period at site 2 in Goose Cove, Newfoundland.

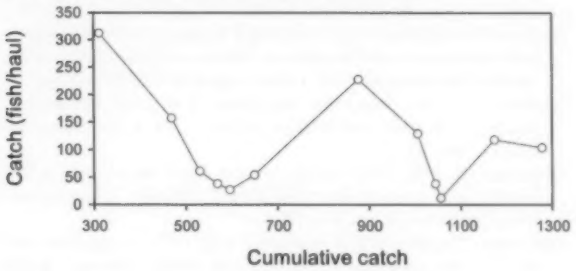
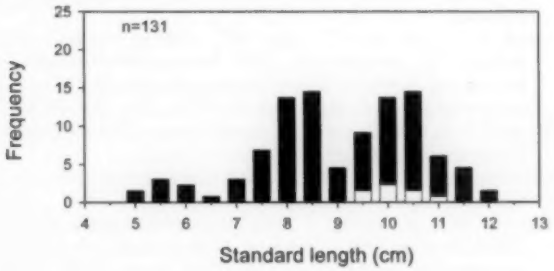


Fig. 7. Length–frequency distribution of postsettled age 0 Atlantic cod captured in Goose Cove, Newfoundland, in March 1995. Open portions of bars represent the length–frequency distribution of marked cod.



to saturate the eelgrass habitat during a year of high abundance, resulting in significant exclusion of cod which settled later in the season. It has been suggested that cod settling when the most suitable shelter sites are already saturated may be forced to occupy less suitable refuge sites (Tupper and Boutilier 1995*a*), and as a result, they may suffer higher predation mortality. Evidence of greater predation risk in nearshore environments at night (Pihl 1982; Keats 1990; Clark and Green 1990; Grant and Brown 1998) suggests that competitive processes associated with availability of suitable shelter sites may be highest for age 0 cod at dusk or shortly thereafter. Competition for available resting sites has been documented for diurnal fish (Robertson and Sheldon 1979), suggesting that nocturnal shelter sites may constitute resting territories. Age 0 cod may compete for suitable shelter sites in coastal environments and increased body size may result in a competitive advantage (Tupper and Boutilier 1995*a*, 1995*b*). Subsequently, in coastal regions where adequate shelter sites are limited, postsettlement processes may influence the contribution of later settlement pulses to the population in years/locations where strength of the first settlement pulse is high.

Nearshore studies on the movements of age 0 cod indicate that site fidelity may be relatively high (site attached and territorial; Tupper and Boutilier 1995*a*) or low (formation of localized shoals; Olsen and Soldal 1989; this study) and varying levels of predation risk may result in both modes of behaviour being adopted within a given region (Tupper and Boutilier 1995*a*). If individual age 0 cod are typically solitary and site attached (Tupper and Boutilier 1995*a*), then they should only shoal when it is advantageous to do so (Pitcher 1986). The

Table 3. Mark–recapture abundance estimates for postsettled age 0 Atlantic cod in Goose Cove, Newfoundland, during September 1994 (GC-1994-1), November 1994 (GC-1994-2), and September 1995 (GC-1995) and at Sunnyside, Newfoundland, in October 1994 (SS-1994).

Location	*R*	*C*	*M*	*N*
GC-1994-1	24	880	667	24 457 (16 488 – 38 114)
GC-1994-2	17	316	654	12 157 (7 598 – 20 875)
GC-1995	44	185	1188	4 995 (3 725 – 6 868)
SS-1994	29	135	624	2 905 (2 025 – 4 342)

Note: *R* is the number of marked cod in the recapture sample, *C* is the number of cod in the recapture sample, *M* is the number of cod marked in the population, and *N* is the population estimate. The 95% CIs (in parentheses) were calculated from a Poisson frequency distribution.

Table 4. Beach seine catches (number per haul) of age 0 and age 1 Atlantic cod during diel sampling at site 2 in Goose Cove, Newfoundland, September and October 1994.

	September 24		September 30		October 8	
Time	Age 0	Age 1	Age 0	Age 1	Age 0	Age 1
09:00	302 (—)	18	77 (11)	26	364 (20)	20
12:00	416 (79)	21	191 (13)	19	762 (25)	15
15:00	445 (75)	19	479 (13)	15	278 (14)	16
18:00	325 (22)	18	187 (5)	26	393 (7)	10
21:00*	94 (7)	35	49 (1)	27	66 (2)	33
24:00*	71 (7)	38	42 (2)	35	— (—)	—
03:00*	74 (2)	52	49 (2)	47	42 (1)	28
06:00*	61 (2)	39	29 (0)	38	26 (0)	32
09:00	368 (42)	29	316 (10)	20	1028 (42)	11

Note: Values in parentheses are the number of marked age 0 cod recaptured in the sample; —, no data. Note that 667 cod were marked and released at site 2 by 11:00 on September 24, 1994.

*Nocturnal sample.

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decision to join a shoal will depend on local biotic factors such as cohort abundance, prey availability, and predation risk. For example, when in the presence of few conspecifics, cyprinids seek refuge from a predator, but shoal when enough conspecifics are present (Pitcher 1986). Circumstances that lead to social behaviour in age 0 cod may vary from one region to another such that detection of variation in year-class strength and geographic contraction across a large coastal area (numerous bays along coastal Newfoundland; Schneider et al. 1997) may be confounded by local variation in behaviour. Evidence of local inshore populations of cod in bays surrounding insular Newfoundland (Hutchings et al. 1993) and bay-to-bay differences in abundance of juvenile cod (Schneider et al. 1997) suggest that behavioural differences may be important. Although coastal populations of age 0 cod may exhibit site fidelity, bulk movements within local habitats may affect the vulnerability of age 0 cod to beach seine surveys based on single point-in-time (i.e., annual) site samples conducted during the day. If shoaling is widespread in coastal Newfoundland, where the shoreline consists largely of steep cut banks with narrow beach areas, then annual nearshore beach seine surveys on the distribution and abundance of age 0 cod may benefit when numerous proximal site samples are conducted within a given habitat.

Olsen and Soldal (1989) observed a diurnal activity cycle, zooplanktivory, and localized schooling by age 0 cod on the Finnmark coast of Norway. In Norway, very large schools were distinguishable 2–3 m off the bottom at depths of 20–30 m by echosounder during the day and density was often highest close to the rocky shoreline. In coastal Newfoundland, the highest densities of age 0 cod have been located at depths of 4–7 m in recent years (Methven and Schneider 1998). If this apparently restricted distribution is related to the recent collapse of the northern cod stock, then a rebuilding of this stock may result in increased alongshore distribution of age 0 cod, followed by expansion into deeper waters where acoustic studies may be more practical (Olsen and Soldal 1989).

Studies of juvenile fish are increasingly supplying evidence that specific habitat requirements must be met in order to attain high recruitment. Current findings suggest that in coastal waters, age 0 cod shoal and feed locally during the day on or near structurally complex bottom habitat and settle on these habitats at night for protection from predators. Additional information is needed on the extent of predation mortality in coastal regions, such as effects of year-to-year variation in strength of autumnal settlement pulses of age 0 cod on movement rates and extent of cannibalism by older juveniles in shallow-water habitats at night.

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References

Bogstad, B., Lilly, G.R., Mehl, S., Pálsson, Ó.K., and Stefánsson, G. 1994. Cannibalism and year-class strength in Atlantic cod (*Gadus morhua* L.) in Arcto-boreal ecosystems (Barents Sea, Iceland, and eastern Newfoundland. ICES Mar. Sci. Symp. **198**: 576–599.

Clark, D.S., and Green, J.M. 1990. Activity and movement patterns of juvenile Atlantic cod, *Gadus morhua*, in Conception Bay, Newfoundland, as determined by sonic telemetry. Can. J. Zool. **68**: 1434–1442.

Gotceitas, V., and Brown, J.A. 1993. Substrate selection by juvenile Atlantic cod (*Gadus morhua*): effects of predation risk. Oecologia, **93**: 31–37.

Gotceitas, V., Fraser, S., and Brown, J.A. 1997. Use of eelgrass beds (*Zostera marina*) by juvenile Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **54**: 1306–1319.

Grant, S.M., and Brown, J.A. 1998. Diel foraging cycles and interactions among juvenile Atlantic cod (*Gadus morhua*) at a nearshore site in Newfoundland. Can. J. Fish. Aquat. Sci. **55**. This issue.

Hawkins, A.D., Soofiani, N.M., and Smith, G.W. 1985. Growth and feeding of juvenile cod (*Gadus morhua* L.). J. Cons. Cons. Int. Explor. Mer, **42**: 11–32.

Helfman, G.S. 1986. Fish behaviour by day, night and twilight. *In* The behaviour of teleost fishes. *Edited by* T.J. Pitcher. Chapman and Hall, London, U.K. pp. 366–387.

Hutchings, J.A., Myers, R.A., and Lilly, G.R. 1993. Geographic variation in the spawning of Atlantic cod, *Gadus morhua*, in the Northwest Atlantic. Can. J. Fish. Aquat. Sci. **50**: 2457–2467.

Keats, D.W. 1990. A nocturnal inshore movement of juvenile cod *Gadus morhua* L. in eastern Newfoundland. J. Exp. Mar. Biol. Ecol. **139**: 167–173.

Lima, S.L., and Dill, L.M. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. Can. J. Zool. **68**: 619–640.

Lough, R.G., Valentine, P.C., Potter, D.C., Auditore, P.J., Bolz, G.R., Neilson, J.D., and Perry, R.I. 1989. Ecology and distribution of juvenile cod and haddock in relation to sediment type and bottom currents on eastern Georges Bank. Mar. Ecol. Prog. Ser. **56**: 1–12.

MacCall, A.D. 1990. Dynamic geography of marine fish populations. University of Washington Press, Seattle, Wash.

Magurran, A.E., and Higham, A. 1988. Information transfer across fish shoals under predator threat. Ethology, **78**: 153–158.

Methven, D.A., and Bajdik, C. 1994. Temporal variation in size and abundance of juvenile Atlantic cod (*Gadus morhua*) at an inshore site off eastern Newfoundland. Can. J. Fish. Aquat. Sci. **51**: 78–90.

Methven, D.A., and Schneider, D.C. 1998. Gear-independent patterns of variation in catch of juvenile Atlantic cod (*Gadus morhua*) in coastal habitats. Can. J. Fish. Aquat. Sci. **55**. In press.

Olsen, S., and Soldal, A.V. 1989. Observations on inshore distribution and behaviour of 0-group northeast Arctic cod. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **191**: 296–302.

Perry, G., and Pianka, E.R. 1997. Animal foraging: past, present and future. Trends Ecol. Evol. **12**: 360–364.

Pihl, L. 1982. Food intake of young cod and flounder in a shallow bay on the Swedish west coast. Neth. J. Sea Res. **15**: 419–432.

Pinsent, D.L., and Methven, D.A. 1997. Protracted spawning of Atlantic cod (*Gadus morhua*) in Newfoundland waters: evidence from otolith microstructure. Can. J. Fish. Aquat. Sci. **54**(Suppl. 1): 19–24.

Pitcher, T.J. 1986. Functions of shoaling behaviour in teleosts. *In* The behaviour of teleost fishes. *Edited by* T.J. Pitcher. Chapman and Hall, London, U.K. pp. 294–337.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. No. 191.

Riley, J.D., and Parnell, W.G. 1984. The distribution of young cod. *In* The propagation of cod, *Gadus morhua* L. *Edited by* E. Dahl,

© 1998 NRC Canada

D.S. Danielssen, E. Moksness, and P. Solemdal. Flød. Rapp. **1**: 563–580. (ISSN 0333–2594)

Robb, A.P. 1981. Observations on the food and diel feeding behaviour of pelagic 0-group gadoids in the northern North Sea. J. Fish Biol. **18**: 183–194.

Robertson, D.R., and Sheldon, J.M. 1979. Competitive interactions and the availability of sleeping sites for a diurnal coral reef fish. J. Exp. Mar. Biol. Fish. **3**: 109–128.

Robson, D.S., and Regier, H.A. 1964. Sample size in Petersen mark–recapture experiments. Trans. Am. Fish. Soc. **90**: 181–189.

Schneider, D.C., Methven, D.A., and Dalley, E.L. 1997. Geographic contraction in juvenile fish: a test with northern cod (*Gadus morhua*) at low abundances. Can. J. Fish. Aquat. Sci. **54**(Suppl. 1): 187–199.

Siegel, S. 1956. Nonparametric statistics for the behavioural sciences. McGraw-Hill, New York.

Støttrup, J.G., Nielsen, J.R., Krog, C., and Rasmussen, K. 1994. Results on the extensive production of North Sea cod, *Gadus morhua* L., and their growth and distribution subsequent to release in Limfjord, Denmark. Aquat. Fish. Manage. **25**(Suppl. 1): 143–160.

Swain, D.P. 1993. Age- and density-dependent bathymetric pattern of Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. **50**: 1255–1264.

Swain, D.P., and Wade, E.J. 1993. Density-dependent geographic distribution of Atlantic cod (*Gadus morhua*) in the Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. **50**: 725–733.

Taggart, C.T., Anderson, J., Bishop, C., Colbourne, E., Hutchings, J., Lilly, G., Morgan, J., Murphy, E., Myers, R., Rose, G., and Shelton, P. 1994. Overview of cod stocks, biology, and environment in the northwest Atlantic region of Newfoundland, with emphasis on northern cod. ICES Mar. Sci. Symp. **198**: 140–157.

Tupper, M., and Boutilier, R.G. 1995*a*. Size and priority at settlement determine growth and competitive success of newly settled Atlantic cod. Mar. Ecol. Prog. Ser. **118**: 295–300.

Tupper, M., and Boutilier, R.G. 1995*b*. Effects of habitat on settlement, growth, and postsettlement survival of Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **52**: 1834–1841.

Zar, J.H. 1984. Biostatistical analysis. Prentice Hall, Englewood Cliffs, N.J.

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Estimating gillnet selectivity using nonlinear response surface regression

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Abstract: We present a method of estimating the selectivity of experimental gill nets in which type A and type B curves are solved for simultaneously as a response surface using nonlinear regression. The modeling approach provides a general statistical framework for estimating selectivity parameters, evaluating different functional forms of the selectivity model, and testing for differences between models. We applied this approach to the gillnet catches of Louisiana spotted seatrout (*Cynoscion nebulosus*) in a five-panel experimental net from data collected from 1988 to 1995. The selectivity of the experimental gill nets for female and male spotted seatrout could be described by a common response surface that was based on a four-parameter normal probability density function ($r^2 = 0.95$). By estimating type A and type B curves simultaneously the model was able to explain 74% more variation in the data than when compared with methods that estimate type B curves for each size-class individually. Statistical comparison of annual response surfaces was not significantly different ($p > 0.05$) and suggests that the estimation approach was relatively insensitive to interannual variation in population size composition.

Résumé : Nous présentons une méthode d'évaluation de la sélectivité des filets maillants expérimentaux dans laquelle les courbes de type A et de type B sont résolues simultanément comme des surfaces de réponse par une régression non linéaire. La modélisation offre un cadre de travail statistique général pour estimer les paramètres de sélectivité, évaluer les différentes formes fonctionnelles du modèle de sélectivité et rechercher les différences entre les modèles. À partir de données recueillies entre 1988 et 1995, nous avons appliqué cette approche aux captures d'acoupa (*Cynoscion nebulosus*) de la Louisiane effectuées à l'aide d'un filet maillant expérimental à cinq panneaux. La sélectivité des filets pour les acoupas femelles et mâles pourrait être décrite par une surface de réponse fondée sur une densité de probabilité normale à quatre paramètres ($r^2 = 0{,}95$). En calculant simultanément les courbes de type A et de type B, le modèle expliquait 74% de plus de la variation dans les données que lorsqu'il était comparé à des méthodes qui calculent les courbes de type B pour chaque classe de taille. La comparaison statistique des surfaces de réponse annuelle n'était pas significativement différente ($p > 0{,}05$), et la stratégie d'évaluation serait relativement insensible à la variation interannuelle de la composition de la population selon la taille. [Traduit par la Rédaction]

Introduction

Experimental gill nets are a widely used research tool to sample fish populations. Because gill nets are highly size selective, bias in population descriptors that imply random sampling such as growth, mortality, and abundance can be introduced (Hamley 1975). Size-selective bias can be circumvented, to some extent, by fishing a series of different-sized meshes simultaneously so that a broader range of sizes of fish in the population are captured. Even this, however, does not ensure a truly representative sample of the fish population and effort must be made to correctly estimate the selectivity of each mesh in the experimental gill net. Once mesh selectivity is estimated, the catches of fish in the experimental gill net can be adjusted for the effect of mesh selectivity, thereby giving an estimate of the corrected size composition of the population from which the sample was drawn (McCombie and Fry 1960; Gulland and Harding 1961; Ricker 1975).

Direct estimates of gillnet selectivity can be obtained from sampling a fish population with known size composition. However, indirect methods to estimate selectivity must be used if the size structure of the population is not known or cannot be reliably estimated (i.e., with tag and recapture studies). Since Baranov's (1948) pioneering work on gillnet selection theory, a myriad of methods and models have been proposed to indirectly estimate the selectivity of gill nets. Most indirect methods follow one of two basic approaches: the use of "type A" curves with methods developed by Olsen (1959), Holt (1963), and Hamley and Regier (1973) or methods that use "type B" curves as intermediaries such as those of Baranov (1948), McCombie and Fry (1960), and Regier and Robson (1966).

Regier and Robson (1966) defined type A selectivity to represent the probability of capture of one mesh size to various size-classes of fish, while type B selectivity gives the probability of capture of a single size-class of fish to different meshes. With suitable assumptions, various mathematical models have been used to describe either type A and type B selectivity curves. The advantage of type B curves is that estimates of selectivity are not affected by different size-class abundances because catches of each mesh for a given size-class of fish are proportional to selectivity for that size (Hamley 1975); therefore, selectivity should be unbiased. Regier

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Table 1. Number of Louisiana spotted seatrout caught in various mesh sizes of experimental gill nets used for selectivity analysis in this study, 1988–1995.

	Mesh size (cm)					
Year	5.1	6.4	7.6	8.9	10.2	Total
1988	1770	2559	1369	427	141	6266
1989	1590	2147	1114	472	157	5480
1990	1350	1253	687	205	34	3529
1991	1825	2163	839	206	41	5073
1992	1358	1812	1092	223	71	4556
1993	1336	1987	1001	271	84	4679
1994	1426	1559	672	191	63	3911
1995	1677	1762	738	264	98	4539

and Robson (1966) found that their computational approach to indirectly estimate type B curves provided better estimates than other approaches using type A curves based on a known standard. Problems still remain with using type B curves as intermediaries because existing methods either involve some degree of subjectivity in fitting the data or the statistical properties of the selectivity estimates and estimation methodology to derive final type A curves are unknown.

In this paper, we extend the approach of Regier and Robson (1966) by estimating type A and type B curves simultaneously as a response surface using nonlinear regression. This modeling approach provides a general statistical framework for evaluating different probability distributions to describe selectivity. It is also tractable in terms of assessing reliability (precision) of the parameter estimates and the mathematical model used to describe selectivity. While the statistical properties of nonlinear regression are well known (Bard 1974), its use as we have applied it to estimate gillnet selectivity as a response surface is unique. Therefore, we examined the statistical properties of this estimation methodology using new techniques in bootstrapping (Efron and Tibshirani 1993).

Materials and methods

Sampling and gillnet data

This study was based on experimental gillnet data obtained from a coastal finfish monitoring program conducted by the Louisiana Department of Wildlife and Fisheries. State biologists used a "run-around" method to capture spotted seatrout (*Cynoscion nebulosus*) in monofilament nylon experimental gill nets in one of five possible mesh sizes: 2.0, 2.5, 3.0, 3.5, and 4.0 in. (5.08, 6.35, 7.62, 8.89, and 10.16 cm, respectively) stretch measure (Table 1). Fish entangled in the nets (<4%), identified as those held in the net anterior to the gill covers or on body protrusions, were excluded from analysis. A brief description of fishing and data collection procedures will be provided here; however, readers interested in specific methodology should consult Adkins and Bourgeois (1982).

Data were collected by teams of biologists within seven hydrographic study areas covering the entire coastal zone of Louisiana. About 8–14 stations within each study area were sampled twice monthly between January and October from 1988 to 1995. Stations were chosen at fixed locations along transects extending from brackish marshes (0–9 ppt) to higher-salinity beaches and lower bays (15–30 ppt) of the Louisiana coastal zone, typical of spotted seatrout habitat (Helser et al. 1993). At each station, experimental gill nets, measuring 750 ft (228.5 m) in length (150 ft per mesh panel), were deployed by biologists and encircled about three times by the fishing vessels to drive fish into the nets. The nets were then retrieved, starting with the panel first entering the water, and the catch enumerated by mesh. Fish were measured to the nearest millimetre, weighed to the nearest gram, and examined for stomach content and maturity stage.

List of symbols

- μ_j optimum mesh size for size-class j
- σ_j standard deviation of optimum mesh size for size-class j
- q_j skewness coefficient of optimum mesh size for size-class j
- l_j mean size of fish in size-class j
- m_i size of mesh i, specifically stretch measure (centimetres)
- n_{ij} catch of fish of size-class j in mesh i
- n_j total catch of fish in size-class j
- s_{ij} selectivity of mesh i for fish of size-class j; type B curves with same area
- S_{ij} standardized selectivity of mesh i for fish of size-class j, i.e., $s_{ij}/\max(i)s_{ij}$; type B curves with same height
- π_{ij} observed proportion of total catch in size-class j occurring in mesh i, calculated $n_{ij} / \sum_i n_{ij}$ and corresponds to estimated selectivity s_{ij}
- Π_{ij} standardized observed catches of mesh i for fish of size-class j, calculated $n_{ij}/\max(i)n_{ij}$ and corresponds to standardized estimated selectivity S_{ij}
- N_j relative number of fish of size class j in the population

The skew-normal probability density function is

$$(1)\quad s_{ij} = \frac{1}{\sigma_j\sqrt{2\pi}} \exp^{-(m_i-\mu_j)^2/2\sigma_j^2} x \left\{1 - \tfrac{1}{2}q_j\sigma_j^{3/2}\left[\frac{(m_i-\mu_j)}{\sigma_j} - \frac{(m_i-\mu_j)^3}{3\sigma_j^3}\right]\right\}$$

Model assumptions and development

The selectivity of a gill net for each size of fish may be defined as the probability that, if a fish of a given size encounters the net, it is captured and retained in the net by a unit operation of fishing (Hamley 1975). If the fishing powers of the nets are known or can be reliably estimated, then absolute selectivity can be determined. Probabilities of capture associated with absolute selectivity can almost never be estimated; therefore, it is conventional to work with relative selectivity by making several simplifying assumptions.

First, it is usually assumed that each net has equal fishing power, i.e., each net caught the same proportion of fish of the size-class for which that mesh is most efficient (curve peaks all equal to 1). Although this condition may not always be satisfied, it is usually assumed because robust estimates of selectivity and fishing power cannot be simultaneously estimated (Kirkwood and Walker 1986) from the catch data alone. Second, it is assumed that encounter rates of fish for each size-class and for each mesh size are equal. Some models have been augmented to explicitly account for changes in encounter probability by incorporating swimming speeds or swimming patterns of fish (Rudstam et al. 1984; Borgstrom and Plahte 1992) into the model formulation. However, this information in our studies on spotted seatrout was not available, and therefore, we assumed that the probability of encounter of fish of a single size was equal with respect to the different meshes fished. This assumption may be reasonably satisfied because the individual meshes themselves were fished with equal effort. Finally, with these two assumptions made, efforts are then directed toward estimating the selectivity (relative) as a function of the capture process itself; fitting an assumed mathematical model to the catches from a particular size-class across the different meshes.

This approach forms the basis for one of the two categories of indirect estimation of selectivity, type B selectivity curve. Hamley (1975) stated that the shape of the type B selectivity curve can be estimated without bias by comparing the catches for fixed size-class across the different mesh sizes. This is because the relative catches of each mesh size for fixed size-class are proportional to type B selectivity. An assumed mathematical model is then fit to the catches to

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estimate the shapes of the type B curves. The traditional type A curves which show the selectivity of a given mesh size to the different size-classes are then obtained by intersecting the curves at right angles to the type B curves (Regier and Robson 1966). Regier and Robson (1966) described several procedures for fitting type B curves as intermediaries, ranging from graphical methods (McCombie and Fry 1960) to computational methods (Regier and Robson 1966). In general, type B curves are estimated separately for each size-class, brought to the same relative scale by transforming their ordinates so that separate curves approximate a single curve, and then fitting a final type B "master" curve from which type A curves are derived. The problem with many of these approaches is that methods for fitting the intermediary type B curves to the data involve some degree of subjectivity and (or) the statistical properties of the final type A curves are unknown and intractable.

To circumvent problems with existing methods, Helser et al. (1991, 1994) proposed a procedure for fitting the type A and type B selectivity curves simultaneously using a nonlinear regression approach. They estimated a response surface of selectivities (capture probabilities) by allowing the moments, μ, σ, and q, from the skew-normal probability density function (Croxton et al. 1967) to link the shapes of the selectivity curves to mesh size. The appeal of this general approach using nonlinear regression is that it takes full advantage of the catch information, allowing the final solution to selectivity to be estimated as a function of both mesh size and size-class, and is tractable in terms of assessing reliability of the parameter estimates. The problem, however, was that they found annual differences in selectivity parameter estimates (Helser et al. 1994) which should be independent of the population size composition.

In this paper, we propose using a slight modification to the procedure that eliminates the effect of size composition on selectivity estimates. This modification involves fitting the selectivity model in which the moments are linked as functions of size-class, rather than functions of mesh size. This approach derives initial parameter estimates as linear functions of size-class (Regier and Robson 1966), but obtains a final solution by fitting the catch data as a function of both size-class and mesh size using nonlinear regression. In addition, we also characterized the statistical properties of the estimation methodology; assessing the accuracy and reliability of the model parameter estimates using bootstrap techniques.

Assume the skew-normal probability density function (eq. 1) to describe the type B selectivity curves. Other probability distributions such as gamma, lognormal, weibull, etc., can be used; however, we chose the skew-normal model because of the skew associated with the distributions of spotted seatrout catches from the meshes in our experimental gang. The skew-normal model also provides an added advantage in that it can be reduced to the normal probability density function if skewness terms are found to be insignificant. Following Regier and Robson (1966), the observed catch data are used to calculate the moments μ, σ, and q of the assumed mathematical model for each size class j:

$$(2)\quad \mu_j = \frac{\sum_i n_{ij} m_i}{\sum_i n_{ij}}$$

$$(3)\quad \sigma_j = \frac{\sum_i n_{ij} [m_i - \hat{\mu}_j]^2}{\sum_i n_{ij}}$$

$$(4)\quad q_j = \frac{\sum_i n_{ij} [m_i - \hat{\mu}_j]^3}{\sum_i n_{ij}}$$

The predicted optimum mesh size for each size-class, $\hat{\mu}_j$, estimated by regression methods is then used in eqs. 3 and 4 above to calculate the second and third moments. Once all values of the moments are calculated, the functional relationships between the moments and size-class j are estimated using multiple linear regression methods. They are given in general form as

$$(5)\quad \hat{\mu}_j = \sum_{k=0}^{p} \mu_k l_j^k + \varepsilon_j$$

$$(6)\quad \hat{\sigma}_j = \sum_{k=0}^{p} \sigma_k l_j^k + \delta_j$$

$$(7)\quad \hat{q}_j = \sum_{k=0}^{p} q_k l_j^k + \tau_j$$

where ε_j, δ_j, and τ_j are independent and identically distributed normal random errors and μ, σ, and q for $k = 0, 1, \ldots, p$ are regression coefficients that provide the initial values for the nonlinear iterative phase of the model. With our data for spotted seatrout, we found a system of three initial equations to express the functional relationship of μ_j, σ_j, and q_j as a linear function of l_j (Fig. 1) using PROC GLM in SAS (SAS Institute Inc. 1985). These are equivalent to eqs. 5–7 without error terms, i.e.,

$$(8)\quad \hat{\mu}_j = \mu_0 + \mu_1 \cdot l_j$$

$$(9)\quad \hat{\sigma}_j = \sigma_0 + \sigma_1 \cdot l_j$$

$$(10)\quad \hat{q}_j = q_0 + q_1 \cdot l_j .$$

Therefore, using the skew-normal model (eq. 1), a six-parameter selectivity model is to be estimated that simultaneously fits π_{ij} or Π_{ij} for fish of size-class j in mesh size i using a nonlinear least-squares estimation procedure. In this analysis, we used the term Π_{ij} as the estimating function based on eq. 1, and it is given as

$$(11)\quad E(\Pi_{ij}) = \exp^{-(m_i - \hat{\mu}_j)^2/2\hat{\sigma}_j^2} \, x \left\{ 1 - 1/2\hat{q}_j \hat{\sigma}_j^{3/2} \left[\frac{(m_i - \hat{\mu}_j)}{\hat{\sigma}_j} - \frac{(m_i - \hat{\mu}_j)^3}{3\hat{\sigma}_j^3} \right] \right\}$$

where moments μ_j, σ_j, and q_j in eqs. 8–10 link the shapes of the selectivity curves to size-class of fish. Fitting the model to Π_{ij} derives estimates of selectivity (S_{ij}) that standardizes type B curves to have equal height. In this case the constant of integration before the exponent is dropped from eq. 1. Type A curves, which will also have unit height, were then obtained by plotting the selectivity of each mesh for different size-classes.

We ran the nonlinear response surface model that seeks a least-squares solution between the expected selectivity (S_{ij}) based on the model and the observed data (Π_{ij}) using PROC NLIN in SAS. The least-squares estimate of θ, labeled $\hat{\theta}$, is the set of parameters that minimizes the sums of squared residuals for normally distributed errors:

$$(12)\quad \mathrm{SS}[\mathrm{Res}(\hat{\theta})] = \sum_{i=1}^{n} [\Pi_i - f(x_i', \hat{\theta})]^2$$

where $f(x_i', \hat{\theta})$ is the functional form of eq. 11 evaluated at the n values of x_i'. We obtained solutions for $\hat{\theta}$ by supplying partial derivatives of the model parameters obtained from MAPLE (1994) to the Marquardt algorithm (Marquardt 1963) in SAS. This nonlinear routine provides a "global solution" to the model parameter estimates as well as prediction errors (95% confidence intervals) associated with the expected value for each value of x_i'. Prediction errors that cannot be estimated from more complex models where partial derivatives of the parameters are difficult to obtain can be found using numerical methods (Helser et al. 1994).

We used likelihood ratio tests (Mendenhall et. al. 1986) and other model performance measures (significance of parameter estimates,

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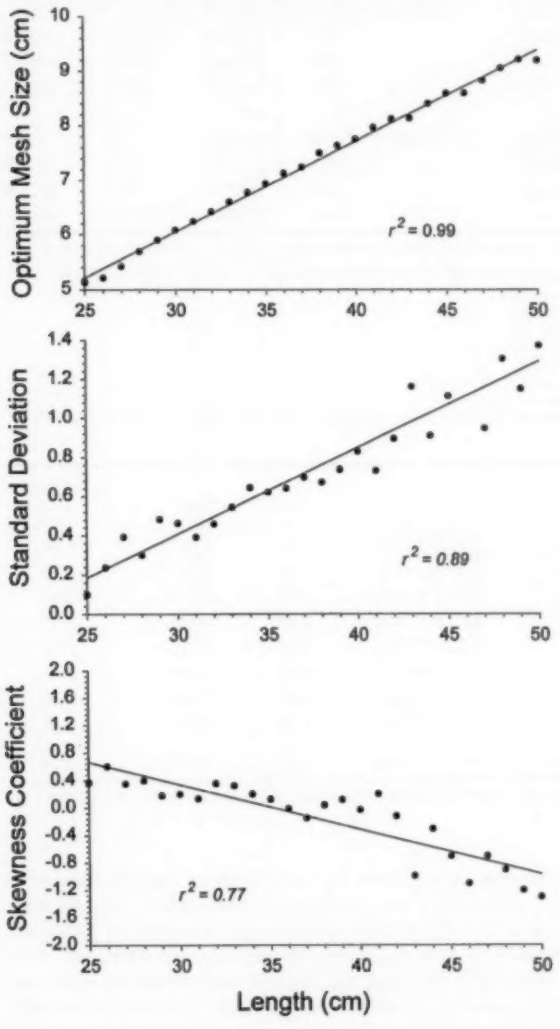
Fig. 1. Relationship between the moments in the skew-normal probability density function and size-class. Predicted (lines) moments, estimated using linear regression, were fit to the calculated moments (points) for each size-class and used as initial parameter estimates in the nonlinear phase of the model.



model r^2) to evaluate whether the six-parameter skew-normal (full model) could be reduced to a family of more simplistic normal models (reduced model). Helser (1992) found different relationships between maximum girth and length of male and female spotted seatrout, so exploring the possibility of different functional forms of the model for the each sex seemed warranted. The functional form of the final model was then fit to years separately and all years (1988–1995) combined to examine interannual variation in the selectivity parameter estimates. Annual differences in the selectivity models were then tested using the likelihood ratio test. In addition, performance measures such as coefficient of determination (r^2), model mean square error (σ^2_{MSE}), and percent reduction in error sums of squares (SSE) were used to evaluate each model. The reduction in SSE, calculated as the percent difference between the initial and final iteration SSE, measures the improved fit to the data that the nonlinear approach provides beyond simply using the initial regression relationships to estimate the type B selectivity curves separately for each size-class.

We then evaluated the statistical properties of this estimation methodology using bootstrap techniques (Efron and Tibshirani 1993). We compared the nonlinear regression output analytically derived from the Marquardt routine in SAS with estimates derived numerically by bootstrapping the vector of model residual errors. From eq. 12, let $r(\hat{e})$ be the vector of model residual errors evaluated at each value x_i' such that

$$(13) \quad r(\hat{e}) = \Pi_i - f(x_i', \hat{\theta}).$$

Then, b bootstrap replications (sets) of sample size n were generated from randomly selecting values from the vector of residual errors $r(\hat{e})$, with replacement from a uniform distribution, and adding these to values of the vector of expected values $S = f(x_i', \hat{\theta})$:

$$(14) \quad x^{*b} = \hat{S} + r(\hat{e}^*)$$

where x^{*b} is the b bootstrap replicate consisting of n psuedo values that were generated from random resampling. The nonlinear selectivity model was then fit to the psuedo data set corresponding to each bootstrap replication to obtain b bootstrap parameter estimates, i.e., $[f(x^{*1}, \hat{\theta}^{*1}) f(x^{*2}, \hat{\theta}^{*2}) \ldots f(x^{*b}, \hat{\theta}^{*b})]$. Expected values of the selectivity parameter estimates and model mean square errors were calculated as the mean, and 95% confidence intervals taken as the 5th and 95th percentiles of the of the empirical distribution based on 1000 bootstrap replications, $b = 1000$. Significant departures in parameters and other statistics between estimates obtained from nonlinear regression output in SAS and from bootstrapping procedures would reveal failure of the model to meet required assumptions, i.e., $e \sim iidN(\mu,\sigma)$. In particular, bias in parameter estimates can arise from correlated error structure (Efron and Tibshirani 1993).

Results

The calculated moments of the assumed mathematical model (skew-normal) to described the selectivity of gill nets for spotted seatrout varied systematically with increasing size-class of fish. The moments, which were calculated for all years combined and for each 1-cm size interval from 25 to 50 cm, were used for subsequent regression analysis. Data less than 25 cm and greater than 50 were sparse for all but the smallest and largest meshes and were excluded. The results of the multiple linear regression analysis to derive initial parameter estimates for the nonlinear phase of the modeling approach indicated that the optimum mesh size (mean) and the standard deviation were strong positive linear functions of size-class (Fig. 1). The coefficients of determination (r^2) were 0.99 and 0.89 for the mean and standard deviation, respectively. The skewness coefficient also exhibited a significant linear relationship with increasing size-class but, in this case, decreased with size (Fig. 1). The lower coefficient of determination ($r^2 = 0.77$) suggested more variation in the third moment. Higher order polynomials did not improve the model fits, and therefore, linear relationships for all moments were used as initial parameter estimates.

Since the regression coefficients relating the skewness parameter to size-class were significant, we used a six-parameter skew-normal model to initiate the nonlinear phase of the modeling and compared it with other more reduced models. For this analysis, we fit four different functional forms of the selectivity model to the gillnet data combined over years for each sex. Results of the nonlinear regression analysis comparing four different functional forms of the selectivity curves indicated that, for both male and female spotted seatrout, the original six-parameter skew-normal model (full model) could be

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Table 2. Comparison of four different functional forms of gillnet selectivity curves for male and female spotted seatrout.

Functional form	Parameter estimates						Nonlinear regression statistics			
	μ_0	μ_1	σ_0^2	σ_1^2	q_0	q_1	r^2	σ^2_{MSE}	$-2\ln\lambda$	$P > \chi^2$
Males										
Skew-normal[a]	0.4835	0.1799	0.3979	0.0127	–1.8565*	0.0193*	0.93	0.0125	—	—
Skew-normal	0.5909	0.1775	0.3659	0.0133	–0.9971	—	0.93	0.0124	1.55	>0.10
Normal	0.4326	0.1861	0.2594	0.0158	—	—	0.91	0.0142	13.85	<0.001
Normal	0.2503	0.1907	0.8383	—	—	—	0.87	0.1700	19.82	<0.001
Females										
Skew-normal	0.6004	0.1791	0.1580	0.0188	–2.0198*	0.0400*	0.95	0.0088	—	—
Skew-normal	0.7355	0.1765	0.1128	0.0198	–0.1566*	—	0.95	0.0089	1.10	>0.250
Normal	0.6757	0.1788	0.0959*	0.0203	—	—	0.93	0.0090	1.94	>0.250
Normal	0.5290	0.1822	0.8565	—	—	—	0.90	0.0143	79.33	<0.001

Note: All functional forms are unit height. Model coefficients of determination (r^2), significance of parameter estimates ($\alpha = 0.05$), and likelihood ratio test statistics ($-2\ln\lambda$) are given for model comparison. Parameter coefficients correspond to the mean ($\hat{\mu}_j = \mu_0 + \mu_1 \cdot l_j$), standard deviation ($\hat{\sigma}_j^2 = \sigma_0^2 + \sigma_1^2 \cdot l_j$), and skewness ($\hat{q}_j = q_0 + q_1 \cdot l_j$). *Parameter estimates not significantly different from zero, $p > 0.05$.

[a]Functional form of model: $S_{ij} = \exp^{-(m_i - \hat{\mu}_j)^2/2\hat{\sigma}_j^2} x \left\{1 - 1/2\hat{q}_j\hat{\sigma}_j^{3/2}\left[\frac{(m_i - \hat{\mu}_j)}{\hat{\sigma}_j} - \frac{(m_i - \hat{\mu}_j)^3}{3\hat{\sigma}_j^3}\right]\right\}$.

Table 3. Model performance measures and gillnet selectivity parameter estimates from the four-parameter normal model by year and for the combined model (1988–1995).

Year	Parameter estimate (standard error)				r^2	σ^2_{MSE}	% Reduction SSE
	μ_0	μ_1	σ_0^2	σ_1^2			
1988	0.372 (0.133)	0.192 (0.003)	0.082 (0.116)*	0.022 (0.003)	0.93	0.012	0.81
1989	0.472 (0.138)	0.186 (0.004)	0.112 (0.118)*	0.021 (0.003)	0.92	0.013	0.72
1990	0.821 (0.160)	0.173 (0.004)	–0.016 (0.137)*	0.025 (0.004)	0.90	0.017	0.63
1991	1.091 (0.171)	0.164 (0.005)	0.124 (0.144)*	0.018 (0.004)	0.85	0.024	0.43
1992	1.057 (0.162)	0.166 (0.004)	0.283 (0.138)	0.015 (0.004)	0.88	0.021	0.54
1993	0.592 (0.151)	0.181 (0.004)	0.155 (0.130)*	0.017 (0.003)	0.89	0.018	0.55
1994	0.464 (0.179)	0.183 (0.005)	0.014 (0.153)*	0.022 (0.004)	0.86	0.023	0.50
1995	0.629 (0.131)	0.179 (0.003)	0.193 (0.111)*	0.016 (0.003)	0.92	0.014	0.61
1988–1995	0.635 (0.109)	0.179 (0.002)	0.124 (0.086)*	0.020 (0.002)	0.95	0.007	0.74

Note: Model performance measures include model r^2, error variance (σ^2_{MSE}), and percent reduction in SSE. *Parameter estimates not significantly different from zero, $p > 0.05$.

reduced to the four-parameter normal model. For both sexes, the five- and six-parameter skew-normal models provided a good fit to the empirical data, with a high coefficients of determination ($r^2 > 0.93$; Table 2). Parameter estimates for the skewness coefficient were not significantly different from zero ($p > 0.05$) for the females as the full model was sequentially reduced by one parameter. The four-parameter normal model fit to the female data provided nearly an equally good fit ($r^2 = 0.93$; Table 2). The likelihood ratio test statistic ($-2\ln\lambda = 1.94$; $p > 0.05$) indicated no loss in explanatory power when reducing the model. For the males, the intercept term associated with the skewness coefficient was significantly different from zero when fitting the five-parameter skew-normal model. The likelihood ratio test also indicated a significant difference by reducing the model further to the four-parameter normal. However, this model was also acceptable for the males because of parsimony with the females (required fewer parameters) and because loss in explanatory power was minimal, as suggested by the high coefficient of determination ($r^2 = 0.91$). Further reduction of the four-parameter normal model to the normal model with equal variance (three-parameter) for both sexes revealed a highly significant difference ($p < 0.001$) with a concurrent reduction in the coefficients of determination ($r^2 = 0.87$ and 0.90). These results suggested that the four-parameter normal model would be appropriate to describe the gillnet selectivity of male and female spotted seatrout where the mean (optimum mesh size) and the standard deviation (selection range) are linear functions of size-class. However, nonsignificant differences ($-2\ln\lambda = 1.20$; $p > 0.05$) when the four-parameter normal model was fit to the sexes separately indicated that selectivity of the gill nets for male and female spotted seatrout could be described by a common response surface.

The four-parameter normal selectivity model was then fit to the gillnet data for each year separately and combined for all years (1988–1995). Nonlinear regression results indicated that the model performed well and provided good fits to each year and for the years combined (Table 3). Coefficients of determination ranged from a low of 0.85 (1991) to a high of 0.93 (1988). In addition, the percent reduction in SSE ranged from a high of 81% in 1988 to a low of 43% in 1991. This indicates that this modeling approach explains more variation in the catch data than from estimating the type B selectivity curves separately for each size-class. Gillnet selectivity parameter estimates for the mean (μ_0, μ_1) were significantly

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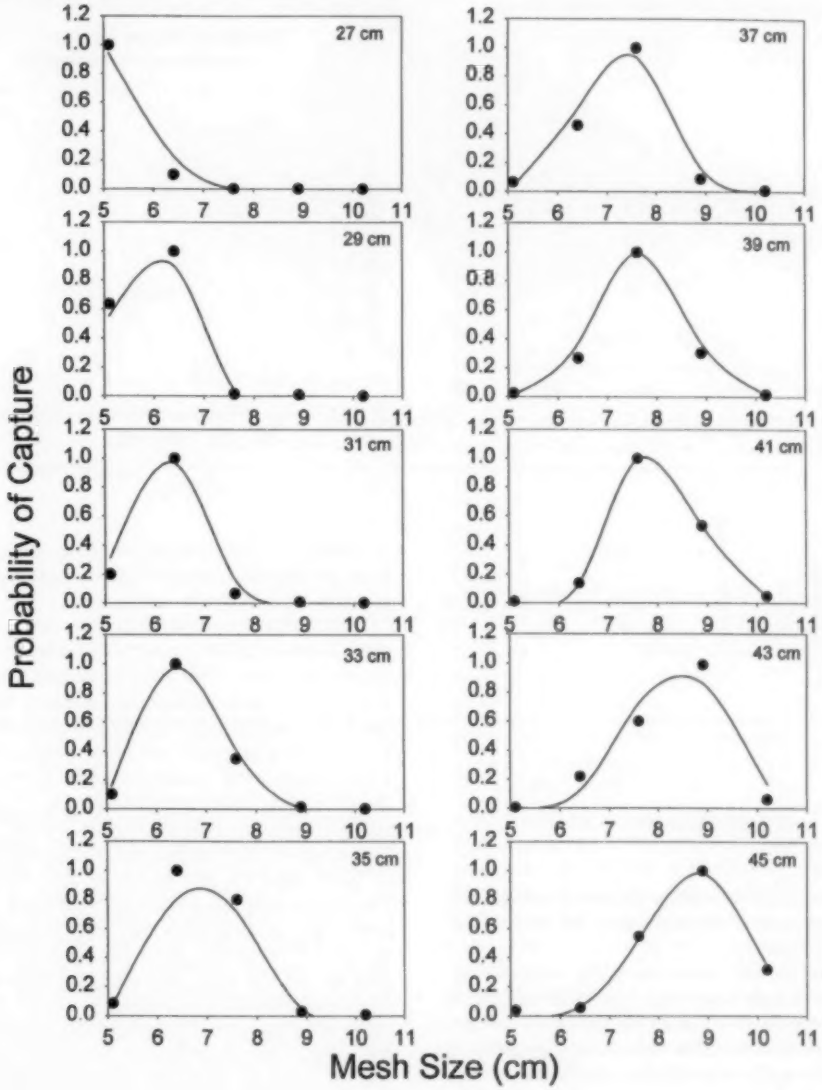
Fig. 2. Type B selectivity curves (probability of capture of various meshes for a single size-class of fish) showing the fit of the final four-parameter normal probability density function to spotted seatrout gillnet catch data (points) estimated using the nonlinear response surface model (lines) (data pooled by year and sex).



different form zero ($p < 0.05$), with the coefficient for the linear term (μ_1) narrowly ranging between 0.164 and 0.192 (Table 3). In addition, parameter estimates corresponding to the linear term (σ_1^2) of the standard deviation (selection range) were also significantly different from zero, ranging from 0.015 to 0.025. Parameter estimates for the intercept coefficient of the standard deviation (σ_0^2) were generally not significantly different from zero.

Theoretically, changes in the population size composition should not affect parameter estimates, since selectivity is proportional to the magnitude of the catches of the meshes within a given size-class. Despite the variation in selectivity parameter estimates between 1988 and 1995, likelihood ratio tests comparing the set of parameter estimates from 1988 and 1990 (the two years most disparate) were not significantly different ($-2 \ln\lambda = 3.01$; $p > 0.05$). Based on these results, we derived final selectivity curves from combining all years (1988–1995). This combined model provided more robust parameter estimates and represents selectivity curves derived from somewhat long-term average conditions in the population. The four-parameter normal model (years combined) fit the observed gillnet data well ($r^2 = 0.95$) and had a 74% reduction in SSE (Table 3). Selectivity parameter estimates were more precise and model error variances smallest of all the models examined. In addition, parameter estimates from this model were all significantly different from zero, with the exception of the

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Fig. 3. Model residual errors for size-class and mesh size showing the fit of the final four-parameter normal probability density function to spotted seatrout gillnet catch data estimated using the nonlinear response surface model (data pooled by year and sex).

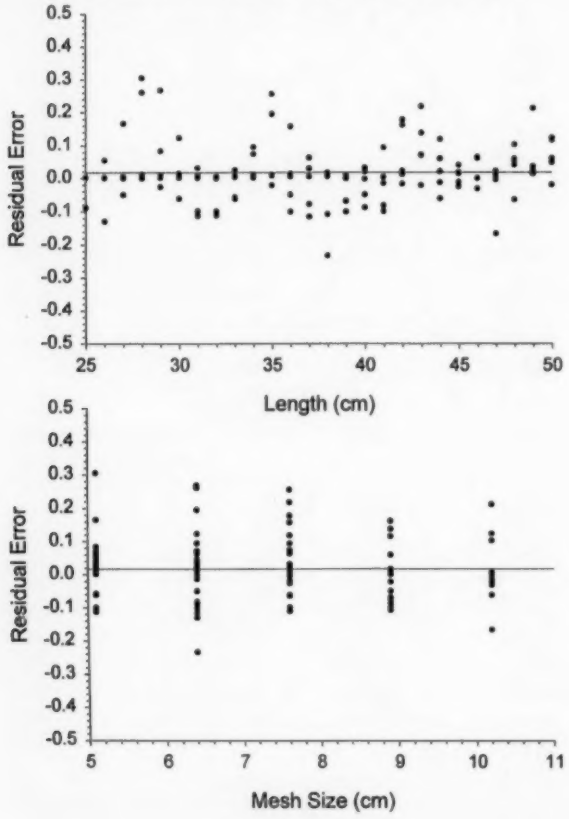
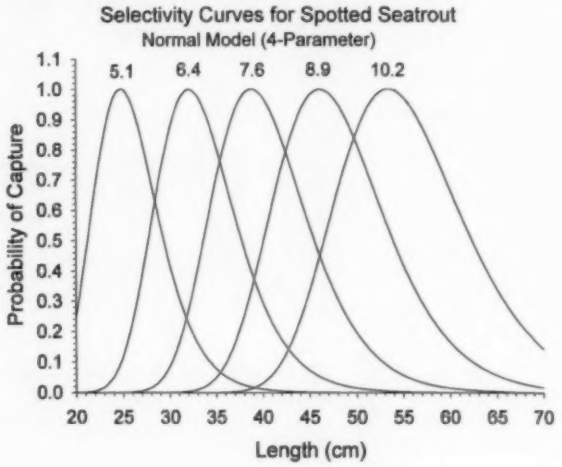


Fig. 4. Type A selectivity curves (probability of capture of single mesh for various sizes of fish) from the final four-parameter normal probability density function estimated using the nonlinear response surface model (data pooled by year and sex).



intercept term for the standard deviation. Expected values were generally intermediate to those estimates from the model fit to the years separately (Table 3).

The four-parameter normal model using the nonlinear approach was flexible enough to provide a good fit of type B selectivity curves to the observed data (Fig. 2). Here, the predicted probabilities of capture of the various meshes for each size-class were in good agreement with the observed data. The shapes of these selectivity curves for groups of adjacent size-classes were, in general, similar, but the optimum mesh size and selection range systematically changed (increased) with increasing size-class. In addition, residual errors from this selectivity model suggest no evidence of lack of fit (Fig. 3) or gross violations of model assumptions. The corresponding type A selectivity curves (Fig. 4), which are viewed at 90° angles to the type B curves, also show that both the mean (optimum selection length) and the standard deviation (selection range) are linear functions of size-class. It is interesting to note that even though the skewness term was not found to be significant when estimating the type B curves, there is a slight positive skew associated with the type A selectivity curves and is probably imparted from the fact that the standard deviation (selection range) for each type B curve increased as a function of size-class. The response surface of capture probabilities from the selectivity model fit to the data across both mesh size and size-class is shown in Fig. 5.

The final four-parameter normal model fit to the gillnet data had robust statistical properties associated with nonlinear parameter estimates. This conclusion was based on the observation that for most parameters estimates the expected values (means), standard errors, and 95% confidence intervals from the analytical method (nonlinear Marquardt algorithm from NLIN) were nearly identical to those from numerical methods (bootstrapping model residual errors) (Table 4). Where parameter estimates differed slightly (i.e., σ_1^2, σ_2^2 and σ_{MSE}^2) between the two approaches, analytical estimates never differed by more than 5% and generally fell within numerical 95% confidence intervals associated with those parameters. These results also translate into very similar prediction errors (95% confidence intervals) about the expected value of selectivity (Fig. 6). On this basis, the nonlinear response surface model applied to estimating selectivity provided reliable and statistically robust parameter estimates. Significant departures in the mean square error between the analytical and numerical methods for deriving variances would probably justify using the bootstrapping procedure for estimating prediction errors.

Discussion

In recent years, gillnet selectivity research has advanced along two general lines, mathematical models to describe selectivity and statistical techniques of estimating selectivity. Since Hamley (1975), few fundamentally different statistical estimation approaches have been proposed (Kirkwood and Walker 1986; Helser et. al. 1991, 1994; Millar and Holst 1997). The approach presented in this paper is an extension to the earlier work by Regier and Robson (1966) who estimated type B selectivity curves for each size-class separately using multiple linear regression. Here, type A and type B selectivity curves were estimated simultaneously (i.e., as a response surface)

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Fig. 5. Response surface of capture probabilities for spotted seatrout from the final four-parameter normal probability density function estimated using the nonlinear response surface model (data pooled by year and sex).

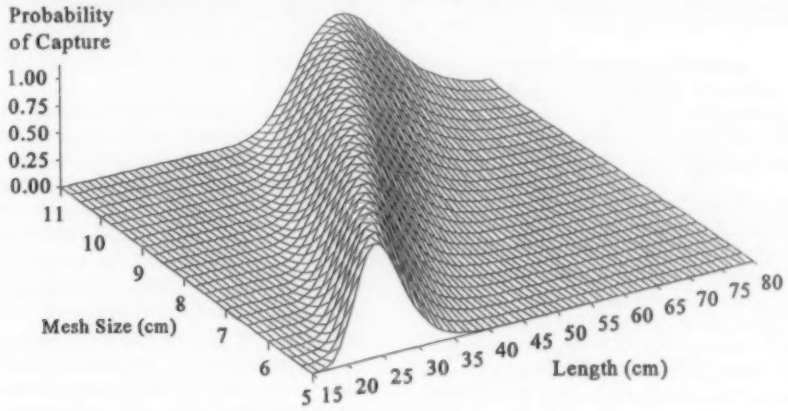

Table 4. Comparison of parameter estimates, 95% confidence intervals (CI) about expected values, and two model performance measures including model mean square error (σ^2_{MSE}) and percent reduction in SSE from analytical and numerical methods of derivation.

	Analytical estimates (NLIN)			Numerical estimates (bootstrap)		
		95% CI			95% CI	
Parameter	Expected value	Lower	Upper	Expected value	Lower	Upper
μ_0	0.6315	0.4336	0.8366	0.6303	0.4478	0.7836
μ_1	0.1799	0.1745	0.1854	0.1801	0.1758	0.1847
σ^2_0	0.1247	–0.0463	0.2958	0.1269	–0.0155	0.2922
σ^2_1	0.0196	0.0149	0.0242	0.0203	0.0163	0.0242
σ^2_{MSE}	0.0071	—	—	0.0068	0.0042	0.0085
% reduction SSE	0.743	—	—	0.695	0.456	0.812

Note: Analytical estimates were obtained from partial derivatives supplied to the nonlinear model, and numerical estimates were obtained from bootstrapping model residual errors.

using nonlinear regression. This technique explained significantly more variation (43–81%) in the observed catch data compared with fitting type B curves to each size-class separately. Several other approaches based on a similar general philosophy of fitting the catch data as a function of both mesh size and size-class have been proposed (Kirkwood and Walker 1986; Millar 1992; Millar and Holst 1997). Our approach differs from these in that we used nonlinear regression as the statistical estimation methodology compared with log-linear or expected maximization (E-M) techniques to fit the assumed selectivity model to the observed catch data. In particular, our approach uses a least-squares implementation procedure to fit a response that is assumed to be based on the normal probability density function and with a normal error structure. These other approaches assume that the catch data are independent Poisson random variates and seek maximum likelihood estimates. Kirkwood and Walker (1986) implemented E-M and maximized on a gamma response whereas Millar (1992) implemented a log-linear model and maximized on several different responses including normal, lognormal, and gamma. It should be noted that different statistical estimation methodologies will give different statistical properties associated with model parameter estimates. While neither technique may be viewed as more appropriate than the other for the general problem of estimating the selectivity of gill nets, our technique, which is based on nonlinear regression, is perhaps more widely used by fishery biologists and is easily implemented. Further, nonlinear regression also has well-known statistical properties (Bard 1974; Gallant 1987), which is essential for evaluating model appropriateness and parameter precision. It is also important to distinguish this paper from those of Helser et al. (1991, 1994). In this analysis, we used the bootstrap technique to assess the statistical accuracy of the nonlinear estimation methodology as it was applied to the problem of estimating gillnet selectivity.

In general, our approach provides a means of examining alternative forms of the selectivity model, testing for differences between years, and evaluating the significance of parameter estimates within a statistical framework (Gallant 1987). Also, model diagnostics such as inspection of residuals, which are easily obtained using existing nonlinear statistical software, can be used to evaluate lack of fit and facilitate model building. For example, the four-parameter normal model fit to the spotted seatrout data indicated no apparent violation of assumptions. This was confirmed by little or no bias in parameter estimates or error variances derived from bootstrapping model residuals. Another advantage is that estimates of prediction errors from the nonlinear model output can be used to generate 95% confidence intervals about the expected value of selectivity. Although this feature is dependent on supplying partial derivatives of the model parameters to the nonlinear algorithm, many computer programs such as

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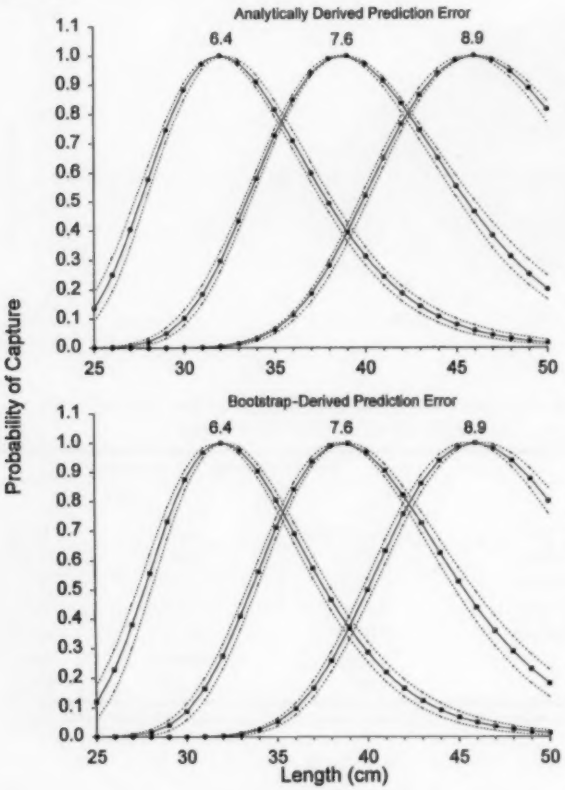
Fig. 6. Comparison of analytically (PROC NLIN) and numerically (bootstrapping residual errors) derived prediction errors around expected values of selectivity for three mesh sizes (6.4, 7.6, and 8.9 cm).



MAPLE are capable of providing them even for rather complex selectivity models. If partial derivatives are not easily obtained, numerical procedures such as bootstrapping model residuals can be used to approximate the empirical prediction errors.

For the data set on spotted seatrout, the four-parameter normal function was chosen as the most appropriate model to describe the gillnet selectivity. It should be noted that the type A selectivity curves generated from the modeling approach presented in this paper differ from those obtained by Helser et al. (1991). The selectivity curves for the larger meshes (7.6, 8.9, and 10.1 cm) were shifted to larger sizes of fish in this study and had less positive skew associated with them. The differences observed here are because the moments of the model were linked as functions of size-class, which help to minimized effects of population size composition on the estimated shape of the curves. In this paper, the type A selectivity curves show that the optimum selection length (mean) increases linearly with increasing mesh size by the proportionality constant, $K = 0.16$ (Fig. 3). This is consistent with Baranov's (1948) theoretical relationship, i.e., $\phi = KL_m$, where ϕ is the mesh size, L_m is the model length of fish captured in the mesh, and K is called the selection factor. Selection factors have been found to vary from 0.10 for slim-bodied fishes such as mackerel to 0.20 for deep-bodied fishes such as bream (Hamley 1975). The type A selectivity curves also reveal that the standard deviation (selection range) is a linear function of mesh size and indicates that the curves are not congruent, an assumption often implied in other indirect methods (Holt 1963).

Another important difference in this paper is that annual selectivity parameter estimates were not significantly different. This is in contrast with our earlier observation that selectivity estimates were significantly different between 1988 and 1990 (Helser et al. 1994) due to a severe winter kill of the spotted seatrout population in 1989. This suggests to us that the effect of population size composition is effectively removed by using the approach presented in this paper. Although some annual variation in selectivity parameter estimates was observed here, this may be due to factors unrelated to changes in population size composition. Some studies have suggested that variation in selectivity may be due to annual changes in fish condition (girth) or fish behavior (Hamley and Reiger 1973; Hamley 1975; Borgstrom and Plahte 1992). Such effects, however, are probably intractable using indirect methods because Borgstrom and Plahte (1992) found that selectivity, when estimated directly from a known population, was still subject to annual variation. Nevertheless, the nonlinear response surface approach presented here provided statistically robust selectivity estimates that were relatively insensitive to annual variation is population size composition. Therefore, selectivity curves can be reliably used to manage the gillnet fishery.

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References

Adkins, G., and Bourgeois, M.J. 1982. An evalution of gill nets for various mesh sizes. La. Dep. Wildl. Fish. Tech. Bull. No. 36.

Baranov, F.I. 1948. Theory and assessment of fishing gear. Pishchepromizdat, Moscow. (Chap. 7. Theory of fishing with gill nets. Transl. from Russian by Ont. Dep. Lands For., Maple, Ont.)

Bard, J. 1974. Nonlinear parameter estimation. Academic Press, New York.

Borgstrom, R., and Plahte, E. 1992. Gillnet selectivity and a model for capture probabilities of a stunted brown trout (*Salmo trutta*) population. Can. J. Fish. Aquat. Sci. **49**: 1546–1554.

Croxton, F.E., Cowden, D.J., and Klein, S. 1967. Applied general statistics. 3rd ed. Prentice-Hall, Englewood Cliffs, N.J.

Efron, B., and Tibshirani, R.J. 1993. An introduction to the bootstrap. Chapman and Hall, New York.

Gallant, A.R. 1987. Nonlinear statistical models. Wiley, New York.

Gulland, J.A., and Harding, D. 1961. The selection of *Clarias mossambicus* (Peters) by nylon gillnets. J. Cons. Perm. Int. Explor. Mer, **26**: 215–222.

Hamley, J.M. 1975. Review of gillnet selectivity. J. Fish. Res. Board Can. **32**: 1943–1969.

Hamley, J.M., and Regier, H.A. 1973. Direct estimates of gillnet selectivity to walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board. Can. **30**: 817–830.

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Helser, T.E. 1992. Development of a quantitative technique for the analysis of the dynamics of fish populations; with an application for spotted seatrout, *Cynoscion nebulosus*, in Coastal Louisisana. Ph.D. dissertation, Louisiana State University, Baton Rouge, La.

Helser, T.E., Condrey, R.E., and Geaghan, J.P. 1991. A new method of estimating gillnet selectivity, with an example for spotted seatrout, *Cynoscion nebulosus*. Can. J. Fish. Aquat. Sci. **48**: 487–492.

Helser, T.E., Condrey, R.E., and Geaghan, J.P. 1993. Spotted seatrout distribution in four coastal Louisiana estuaries. Trans. Am. Fish. Soc. **122**: 99–111.

Helser, T.E., Geaghan, J.P., and Condrey, R.E. 1994. Estimating size composition and associated variances of a fish population for gillnet selectivity, with an example for spotted seatrout (*Cynoscion nebulosus*). Fish. Res. (Amst.), **19**: 65–86.

Holt, S.J. 1963. A method for determining gear selectivity and its application. ICNAF/ICES/FOA Joint Sci. Meet., Lisbon, Contrib. S-15.

Kirkwood, G.P., and Walker, T.I. 1986. Gill net mesh selectivities for gummy shark, *Mustelus antarcicus*, taken in southeastern Australian waters. Aust. J. Mar. Freshwater. Res. **37**: 689–697.

Marquardt, D.W. 1963. An algorithm of least squares estimation of nonlinear parameters. J. Soc. Ind. Appl. Math. **11**: 431–441.

McCombie, A.M., and Fry, F.E. 1960. Selectivity of gill nets for lake whitefish, *Coregonus clupeaformis*. Trans. Am. Fish. Soc. **90**: 176–184.

Mendenhall, W., Scheaffer, R.L., and Wackerly, D.D. 1986. Mathematical statistics with applications. 3rd ed. Duxbury Press, Boston, Mass.

Millar, R.B. 1992. Estimating the size-selectivity of fishing gear by conditioning on the total catch. J. Am. Stat. Assoc. **87**: 962–968.

Millar, R.B., and Holst, R. 1997. Estimation of gillnet and hook selectivity using log-linear models. ICES J. Mar. Sci. **54**: 471–477.

Olsen, S. 1959. Mesh selection in herring gill nets. J. Fish. Res. Board Can. **16**: 339–349.

Regier, H.A., and Robson, D.S. 1966. Selectivity of gillnets, especially to lake whitefish. J. Fish. Res. Board Can. **23**: 423–454.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. No. 191.

Rudstam, L.G., Magnuson, J.J., and Tonn, W.M. 1984. Size selectivity of passive fishing gear: a correction for encounter probability applied to gill nets. Can. J. Fish. Aquat. Sci. **41**: 1252–1255.

SAS Institute Inc. 1985. SAS user's guide: statistics, version 5 ed. SAS Institute Inc., Cary, N.C.

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Benefits and costs of vertical migration by the freshwater copepod *Skistodiaptomus oregonensis*: testing hypotheses through population comparison

David Ghan, K.D. Hyatt, and J.D. McPhail

Abstract: The benefits and costs of vertical migration behaviour of the freshwater lacustrine copepod, *Skistodiaptomus oregonensis*, is explored through the study of two migrating and two nonmigrating populations. The association of vertical migration with the presence of pelagic threespine stickleback (*Gasterosteus aculeatus*) is consistent with the hypothesis that the adaptive benefit of vertical migration by *S. oregonensis* is avoidance of predatory stickleback. The hypothesis of avoidance of juvenile sockeye salmon (*Oncorhynchus nerka*) predation is not supported. *Skistodiaptomus oregonensis* do not migrate in the lake with the highest juvenile sockeye abundance but do migrate in the lake where juvenile sockeye are absent. A foraging efficiency hypothesis does not explain migration behaviour; neither food abundance nor food distribution distinguish lakes where *S. oregonensis* migrate from lakes where they do not migrate. Neither a bioenergetic efficiency hypothesis nor a thermal advantage hypothesis explain migration behaviour; temperature structures are similar in all four lakes examined. Vertical migration appears to be the result of a trade-off between predator avoidance and resource acquisition. Phytoplankton food is less concentrated in the deep habitat where *S. oregonensis* reside during the day. Furthermore, migrators contain less phytoplankton food in their guts than nonmigrators.

Résumé : Nous avons déterminé les avantages et les inconvénients que présente la migration verticale pour le copépode dulcicole lacustre *Skistodiaptomus oregonensis* en étudiant deux populations migrantes et deux populations sédentaires. L'association de la migration verticale avec la présence de l'épinoche à trois épines (*Gasterosteus aculeatus*), un poisson prédateur pélagique, est compatible avec l'hypothèse selon laquelle l'adaptation qui donne lieu à la migration verticale est avantageuse pour *S. oregonensis*, car elle lui permet de se soustraire par évitement à la prédation de l'épinoche. Rien ne vient étayer l'hypothèse selon laquelle la migration verticale permettrait au copépode de se soustraire à la prédation du saumon rouge (*Oncorhynchus nerka*) juvénile. En effet, nous avons constaté que *S. oregonensis* ne migre pas dans le lac où le saumon rouge juvénile est le plus abondant, alors qu'il migre dans le lac où il n'y a pas de saumon rouge juvénile. Par ailleurs, l'hypothèse de l'efficacité de la recherche de nourriture n'explique pas la migration : aux point de vue de l'abondance et de la distribution de la nourriture, il n'y a aucune différence entre les lacs où *S. oregonensis* migre et ceux où il ne migre pas. La migration verticale ne peut être expliquée non plus par le rendement bio-énergétique ou par un facteur thermique; le profil des températures était à peu près le même dans les quatre lacs étudiés. Il semble que la migration verticale soit le résultat d'un compromis entre l'évitement d'un prédateur et la recherche de nourriture. En effet, le phytoplancton est moins concentré dans l'habitat en profondeur où *S. oregonensis* passe la journée. En outre, le système digestif des migrateurs contenait moins de phytoplancton que celui des sédentaires.
[Traduit par la Rédaction]

Introduction

Many pelagic organisms migrate vertically between shallow water at night and deep water during the day. Reverse vertical migrations (between deep water at night and shallower water during the day) are also observed. The literature on such vertical migrations is extensive and dates back more than a century (Ringelberg 1993). Several hypotheses have been advanced to explain the adaptive significance of vertical migration by zooplankton (see reviews of Kerfoot 1985 and Lampert 1989). One, the predator avoidance hypothesis, proposes that migration to deeper, darker water during the day reduces vulnerability to diurnally foraging visual predators (Lampert 1993). Assuming food is less concentrated in deeper water, there may be a feeding opportunity cost associated with vertical migration to avoid predators (Stich and Lampert 1981). An alternative hypothesis, the bioenergetic hypothesis, proposes that cooler temperatures in deeper water reduce metabolic costs and, thus, increase growth (McLaren 1963). A thermal advantage hypothesis (Williamson et al. 1996) proposes that zooplankton move up at night to achieve a higher rate of growth and (or) reproduction at higher temperatures. A fourth hypothesis, the foraging efficiency hypothesis, argues that vertical migrators increase food intake by following a migrating

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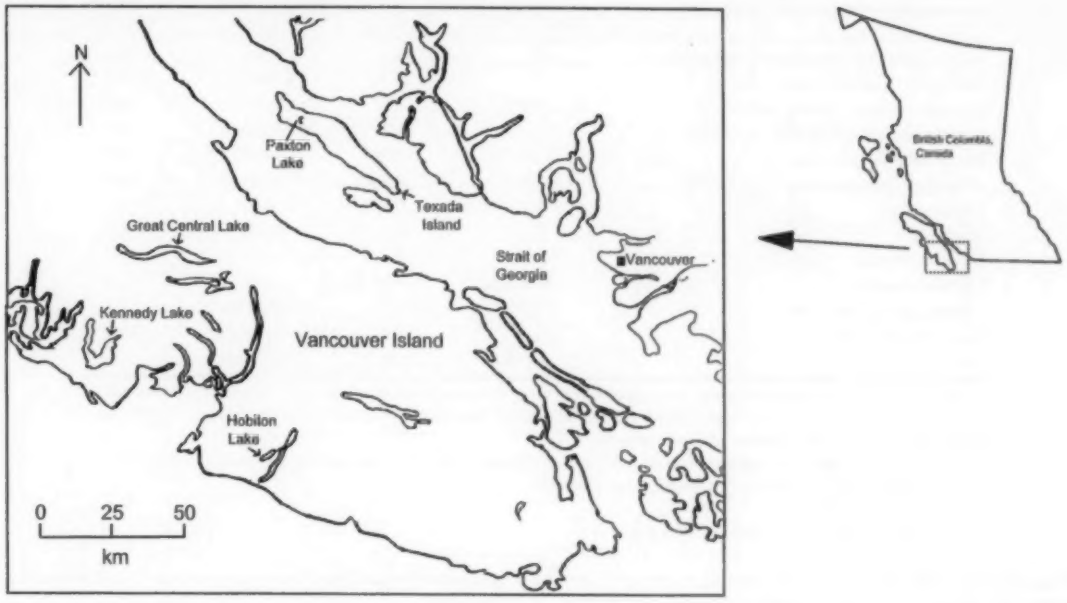
Fig. 1. Location of the four study lakes in southwestern British Columbia.



prey resource (Ketelaars et al. 1995). If the metabolic advantage of residing in cool water during the day is coupled with higher energy intake rates when feeding at night (or during the crepuscular period when prey are more concentrated or of higher quality), there may be a combined foraging and bioenergetic benefit (e.g., Enright 1977; Enright and Honegger 1977).

In this paper, we use a comparative field approach to evaluate each of these hypotheses for the benefits and costs of vertical migration by the zooplankter *Skistodiaptomus oregonensis* in four coastal British Columbia lakes. Such interpopulation comparisons in lakes with relatively simple vertebrate and invertebrate communities provide an opportunity, within the natural environment, to look for associations between vertical migration and factors hypothesized to affect benefits and costs.

Materials and methods

Description of the study lakes

Four study lakes located in south coastal British Columbia (Fig. 1), were sampled from 1992 to 1994 for a "natural experiment" to relate variation in day and night vertical distributions of the copepod *S. oregonensis* among the lakes to differences in fish communities, temperature, food conditions, and other environmental and morphometric factors. Abiotic and biotic conditions in the lakes are compared in Table 1.

In each lake, *S. oregonensis* were common and were the largest zooplankton species present both day and night in the open waters. Cyclopoid species less than 1 mm in total length at maturity and *Bosmina* were also common in all the lakes. *Holopedium* were rare in Great Central Lake, and *Daphnia* were rare in Paxton Lake and Kennedy Lake. Larger macrozooplankton present in the water column only at night were *Neomysis mercedis* in Hobiton and Kennedy lakes and *Chaoborus* in Paxton Lake.

Juvenile sockeye salmon (*Oncorhynchus nerka*) and (or) threespine stickleback (*Gasterosteus aculeatus*) are the only species present offshore in any of the lakes (Table 1). Juvenile sockeye are present in all lakes except Paxton. Paxton and Kennedy lakes contained pelagic stickleback, which did not occur offshore in Hobiton or Great Central Lake.

Zooplankton field collections

To determine the vertical distribution of zooplankton in Kennedy, Great Central, and Hobiton lakes, zooplankton samples were collected simultaneously at depths of 1, 3, 5, 7, 10, 17, and 24 m by towing conical 100-μm Nitex mesh plankton nets attached at intervals along a single rope. Each net was 108 cm long with a 15 cm diameter opening. Tows were 20 min in duration at a speed of 50 cm·s^{-1}. During a tow, an angle of 50° from the horizontal was maintained. A maximum of 40 s passed from the time the first net was released into the water until all nets were in place at the towing depth. Retrieval of the nets required a maximum of 1 min. Thus, relative to the amount of water filtered from the sample depths, nets filtered only small volumes of water during descent and retrieval. Weighted mean depths (WMD) for *S. oregonensis* were calculated from the stratified samples as

$$\mathrm{WMD} = \frac{\sum n_i \Delta_i d_i}{\sum n_i \Delta_i}$$

where n_i is the abundance (individuals per m^3) in the depth interval Δ_i with midpoint d_i (Osgood and Frost 1994). Borders between depth strata were defined as midway between subsequent sample depths. The total number of individuals within each stratum (T_i) is expressed as the number under 1-m^2 surface area and was estimated as

$$T_i = n_i \Delta_i$$

To track changes in *S. oregonensis* vertical distribution during dawn and dusk vertical migrations in Paxton Lake, series of vertically stratified zooplankton hauls were collected for the 9–5, 5–3, and 3–0 m strata in Paxton Lake. The strata were sampled from deepest to shallowest in rapid succession over approximately 8–12 min with a closable double-ringed Wisconsin-style 100-μm Nitex mesh plankton

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Table 1. Biological and physical conditions in four study lakes.

	Great Central	Hobiton	Paxton	Kennedy
Skistodiaptomus oregonensis migration	No	No	Yes	Yes
Pelagic stickleback density (no.·ha^{-1})[a]	0[b]	0[b]	Present[c]	957
Juvenile sockeye density (no.·ha^{-1})[a]	1356	775	0[c]	555
Zooplankton biomass (mg dry weight·m^{-3})	9	11	Unknown	5.4
Mean chl *a* 0–10 m (μg·mL^{-1})	0.291	0.289	1.7	0.339
Annual primary production (g C·m^{-2})	18.9	28.7	Unknown	16.5
Elevation (m)	82	15	61	4
Area (km^2)	51	3.6	0.162	64
Mean depth (m)	212	36	33	16
Light extinction	0.44	0.44	0.5	0.38
Compensation depth (m)	18.5	10.4	Unknown	12.3
Temperature (°C)[d]	18.4	17.8	Maximum 23	18.1
pH	7	6.8	Unknown	7.1

[a]Mean values for 10 annual estimates from 1986 to 1995 via hydroacoustic and trawl surveys in late fall to early winter (K. Hyatt, Fisheries and Oceans Canada, unpublished data). Consult Hyatt et al. (1984) and Hyatt and Stockner (1985) for detail on methods of survey and analysis, respectively.

[b]Although stickleback are present in both Great Central and Hobiton lakes, Fisheries and Oceans Canada trawl surveys over more than a decade indicate their absence from open water.

[c]See McPhail (1993).

[d]Mean temperature June 1 and September 30 at 1 m.

net 292 cm in length with a 55 cm diameter opening. A 20-min interval separated the start of one series of stratified samples and the start of the next series. Upon retrieval, samples were preserved in 4% sugared formaldehyde in 250-mL cylindrical jars.

In the laboratory, subsamples of each sample were taken by stirring the sample jar and then drawing off a measured volume of the sample with a pipette. The subsamples were counted under a Wild M-5 microscope. Species were identified according to Pennak (1989). Each sample was subsampled until either 100 *S. oregonensis* were counted or until the entire sample was counted. Subsampling ceased before counting 100 *S. oregonensis* if the subsample volume exceeded ten times the volume required to count 100 *S. oregonensis* from samples at the other depths from the same sample tow. When lengths were measured, these were recorded with an automated microcomputer-based digitizer system described in Roff and Hopcroft (1986). Metasome length is used in most size class analyses, because it can be measured with greater accuracy than total length.

Measuring food available to *S. oregonensis*

To estimate the depth distribution of food available to *S. oregonensis* in the study lakes, we determined the concentration of chlorophyll *a* extracted from the 3–50 μm size fraction of phytoplankton in lake water from discrete sample depths. This size fraction approximates the size of particles selected by *S. oregonensis* in feeding experiments on lake seston (Vanderploeg 1990) and lake phytoplankton (McQueen 1970). In our samples, lake water was first passed through a 50-μm Nitex mesh to remove larger particles. A measured volume (300–1000 mL) of the remaining filtrate was passed through a 47 mm diameter, 3-μm polycarbonate membrane filter. The membrane was placed in a Petri dish, frozen on dry ice, and retained in the dark. Within 1 week of collection, chlorophyll *a* and phaeopigment were extracted and measured with a Turner model 10-AU spectrofluorometer following the procedure described by Parsons et al. (1984). WMD of chlorophyll *a* depth distributions was calculated using the same method as for zooplankton (eq. 1).

This estimate of available food does not include nonfluorescing alternative food sources (e.g., ciliate protists, heterotrophic flagellates, and fine particulates; Cervetto et al. 1995, Hartmann et al. 1993). Presumably, in freshwater, these alternative prey are more abundant near the surface than below 10 m depth because marine ciliates are found almost exclusively within 5 m of the surface (Jonsson 1989).

Skistodiaptomus oregonensis gut pigment analysis

To estimate feeding activity at the time of collection, the quantity of chlorophyll *a* and phaeopigment in the guts of *S. oregonensis* was determined for Kennedy and Great Central lakes. To compare gut pigments across depth, zooplankton were collected from discrete depths with the horizontal tow method described earlier. To measure changes in gut pigment during dawn and dusk and to compare day versus night gut pigments, vertical hauls from 24 m to the surface were made with the Wisconsin-style plankton net described above. On capture, *S. oregonensis* were collected onto 8 × 8 cm pieces of Nitex mesh, placed in Petri dishes and frozen on dry ice. In the laboratory, samples were thawed in tap water and 10 individual adult *S. oregonensis* were randomly selected, rinsed in distilled water, and placed into 5 mL of 90% acetone and stored overnight in the dark at 5°C. Chlorophyll *a* and phaeopigment concentration in the extract were determined using the same method used for lake water chlorophyll *a* samples.

Results

Vertical distributions of *S. oregonensis* and phytoplankton food resources in the study lakes

In Kennedy Lake, all size-classes of *S. oregonensis* larger than 450 μm were consistent vertical migrators on all survey dates. WMD of *S. oregonensis* in the 750–850 μm metasome length-class (Fig. 2A) was significantly deeper during the day than at night in samples from 1992 to 1994 (paired sample *t* test: $t = 12.805$, $P < 0.001$, $n = 13$).

The WMD for the distribution of the 3–50 μm size fraction of phytoplankton in Kennedy Lake was consistently located near the surface (Fig. 2B) and did not differ significantly from day to night (paired sample *t* test: $t = 2.127$, $0.10 > P > 0.05$, $n = 8$). Except in winter, when density was an order of magnitude lower and the phytoplankton were homogenously distributed down to 24 m, the density of the 3–50 μm size fraction was consistently five to eight times higher in samples at 10 m

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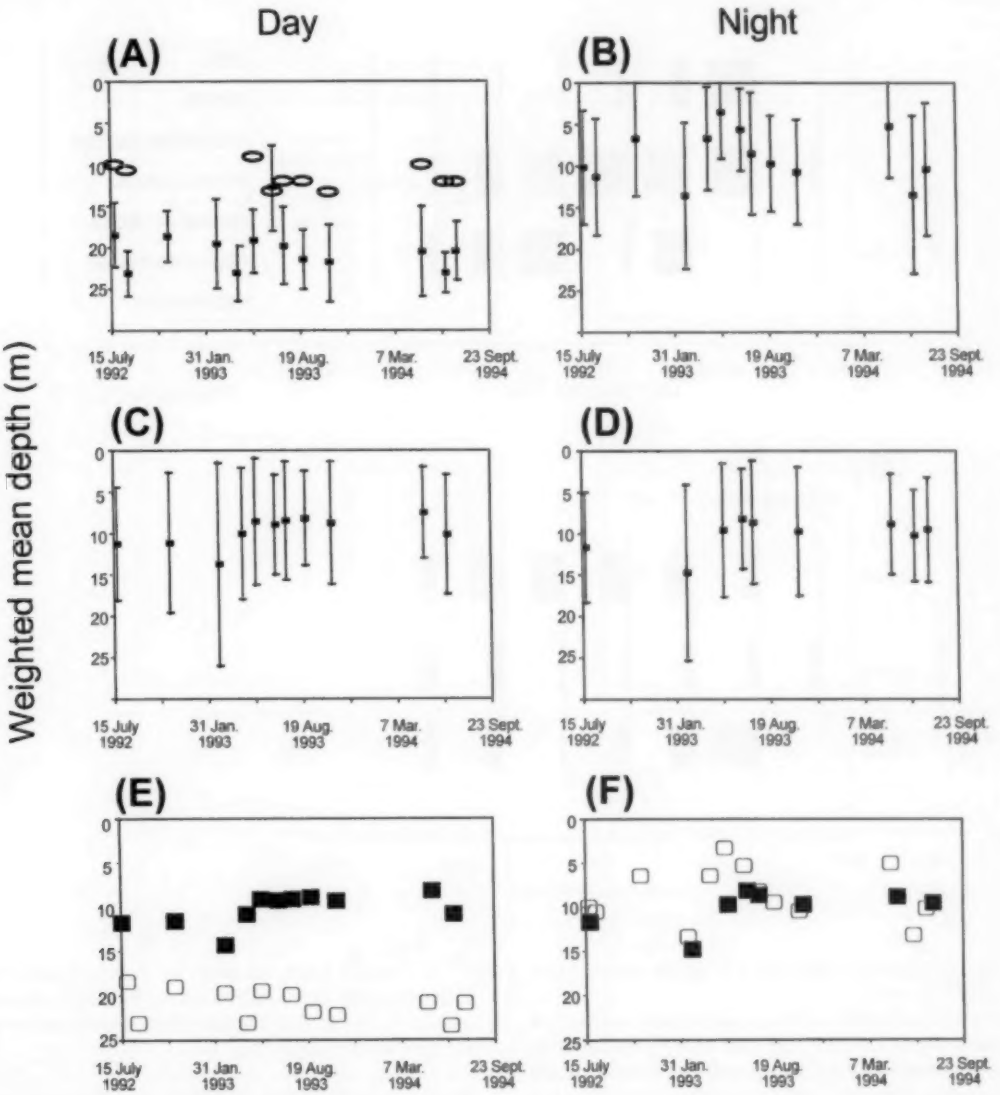
Fig. 2. Day and night weighted mean depths of 750–850 μm *S. oregonensis* (A and B) and the 3–50 μm size fraction of phytoplankton (C and D) in Kennedy Lake on 13 sample dates from 1992–1994. Error bars are SDs for each depth distribution. Ellipses in part A indicate depth of lower part of thermocline when thermal structure was present. In part E and part F, data from parts A, B, C, and D are redrawn to facilitate comparison of the day and night weighted mean depths of *S. oregonensis* (open squares) and the 3–50 μm size fraction of phytoplankton (solid squares).



and above than for samples at 17 and 24 m. During summer stratification, phytoplankton densities declined above the base of the thermocline, which was located at 10–12 m depth. In spring, despite the absence of a strong thermocline, phytoplankton densities decrease at similar depths.

Across sample dates from 1992 to 1994, *S. oregonensis* daytime WMD was significantly below the mean phytoplankton daytime WMD (Fig. 2C; paired sample t test: $t = 9.757$, $P < 0.001$, $n = 11$), while at night, *S. oregonensis* WMD decreased and did not differ from phytoplankton WMD (Fig. 2C; paired sample t test: $t = 1.206$, $0.5 < P < 0.2$, $n = 9$).

In Paxton Lake, *S. oregonensis* were migratory. They were absent from strata above 12 m during the day, ascended to upper strata at dusk, and then descended below 12 m again at dawn (Fig. 3). The density of phytoplankton in the 3–50 μm fraction was similar both day and night (Fig. 3). It peaked between approximately 5 to 11 m and was somewhat lower both nearer the surface and below 11 m to the bottom at 15 m.

Skistodiaptomus oregonensis populations in Great Central and Hobiton lakes did not display migratory behaviour. The WMDs for the distributions of *S. oregonensis* in the 750–850 μm metasome length class did not differ between day

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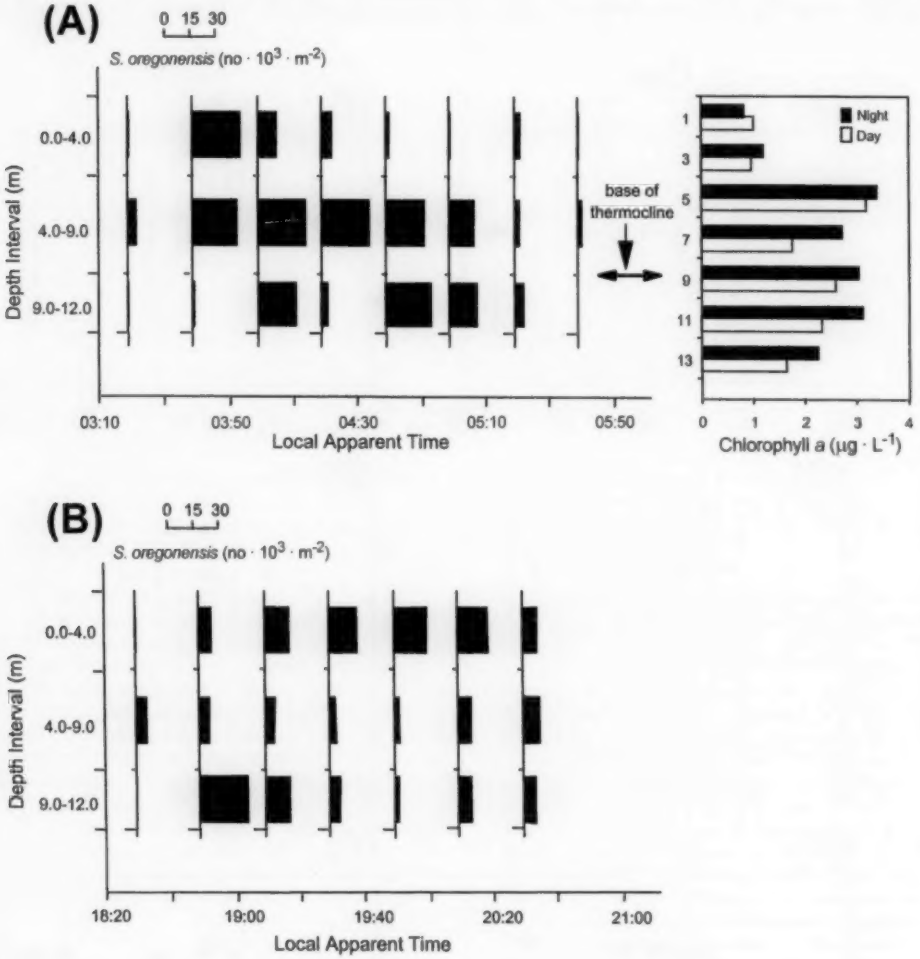
Fig. 3. Changes in density of *S. oregonensis* in three depth strata of Paxton Lake during dawn (A) and dusk (B) on August 19, 1994. For the same sample date, the day and night vertical distributions of chlorophyll *a* from the 3–50 μm size fraction of phytoplankton are shown in part A on the right.



and night in Great Central Lake (Fig. 4A; paired sample *t* test: $t = 0.552$, $P > 0.5$, $n = 6$).

Vertical low, the WMDs of their distributions were below distributions in Great Central (Fig. 4A) were more dispersed both between and across dates, compared with Kennedy Lake (Fig. 2A). During February, April, and May in 1993, when *S. oregonensis* densities were extremely 15 m during the day, during the night, or at both times. These results do not seem to be an artifact of low sample size; at least 40 *S. oregonensis* were counted at the depth of maximum density for each of these distributions.

The WMD of the 3–50 μm size fraction of phytoplankton in Great Central Lake was located in the vicinity of 10–15 m, with no significant difference in mean depths between day and night (Fig. 4B; paired sample *t* test: $t = 2.086$, $0.2 > P > 0.1$, $n = 5$). Figure 4C illustrates the similar mean depth of *S. oregonensis* and the 3–50 μm size class of phytoplankton both day and night.

In Hobiton Lake, all sizes of *S. oregonensis* were nonmigratory. The depth distribution of both large *S. oregonensis* and the 3–50 μm size fraction of phytoplankton were near the surface day and night (Fig. 5).

Body size and vertical distribution of *S. oregonensis* in Kennedy Lake

Both daytime WMD of *S. oregonensis* in Kennedy Lake (Fig. 6A) and the displacement in WMD from night to day (Fig. 6B), increase with metasome length up to approximately 450 μm. Beyond this size, there appears to be little further change. For *S. oregonensis* in size-classes 375 and 425 μm, daytime WMD and displacement in WMD from night to day are highly variable.

Gut pigments and diurnal feeding patterns of migratory and nonmigratory *S. oregonensis*

Migrating *S. oregonensis* from Kennedy Lake contain more

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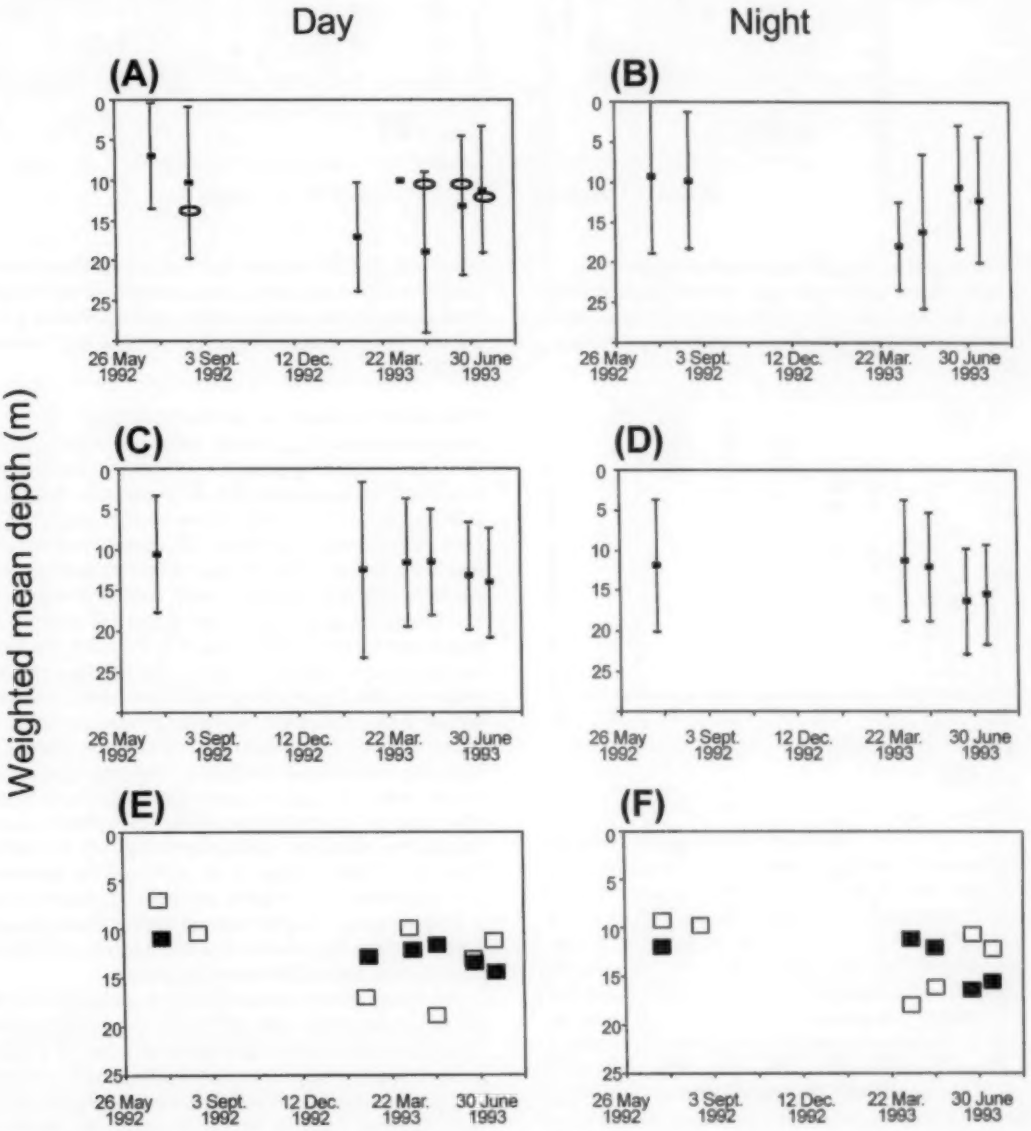
Fig. 4. Day and night weighted mean depths of 750–850 μm *S. oregonensis* (A and B) and the 3–50 μm size fraction of phytoplankton (C and D) in Great Central Lake on seven sample dates from 1992 and 1993. Error bars are SDs for each depth distribution. Ellipses in part A indicate depth of lower part of thermocline when thermal structure was present. In parts E and F, data from parts A and B are redrawn to facilitate comparison of the day and night weighted mean depths of *S. oregonensis* (open squares) and the 3–50 μm size fraction of phytoplankton (solid squares).



chlorophyll *a* and phaeopigment in their guts at night than during the day, while the nonmigrating Great Central Lake population showed no diurnal feeding rhythm (Fig. 7). Within Kennedy Lake, daytime gut pigment concentration decreased with the depth at which *S. oregonensis* were captured (Fig. 8). Gut pigments of the migrating Kennedy Lake population increase at dusk, the time of migration toward the surface, and decrease again at dawn at the time of descent, while nonmigratory Great Central Lake *S. oregonensis* show no such pattern (Fig. 9).

Relationship between weighted mean depth of *S. oregonensis* and chlorophyll *a* concentration in Kennedy Lake

The mean daytime depth of *S. oregonensis* in Kennedy Lake tends to decrease with decreasing mean chlorophyll *a* concentration from the 1-, 3-, 5-, and 7-m depths (Fig. 10). If the two outliers (June 1993 and May 1994) are removed, the mean chlorophyll *a* concentration in the 1-, 3-, 5-, and 7-m samples explains 61% of the variation in the mean depth of *S.*

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Fig. 5. Day (open circles) and night (solid squares) weighted mean depth of 660–795 µm metasome length-class *S. oregonensis* (A) and the 3–50 µm size fraction of phytoplankton (B) in Hobiton Lake on June 25 and August 25, 1992. Error bars are SDs of the population distribution.

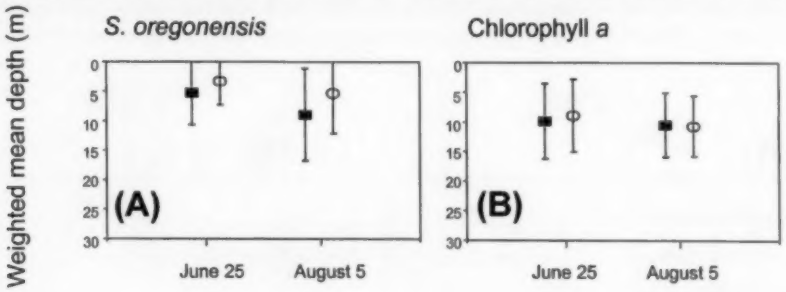
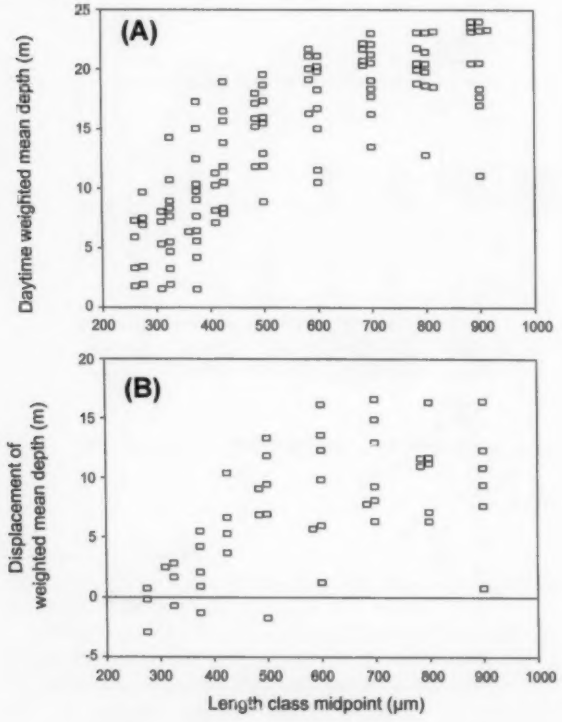


Fig. 6. (A) *S. oregonensis* weighted mean daytime depth versus metasome length-classes in Kennedy Lake. (B) Difference between weighted mean daytime depth and weighted mean night time depth for each sample date. Positive differences indicate greater daytime mean depth.



oregonensis, and the least-squares linear regression is significant ($P < 0.02$).

Discussion

To test the alternative hypotheses for benefits and costs of vertical migration we have sought to relate variation in this behaviour by *S. oregonensis* to environmental factors that are predicted by these various hypotheses to affect the benefits and (or) costs. We argue that only differences in stickleback predation are consistent with differences in vertical migration behaviour and that several alternative hypotheses are not supported. Vertical migration is associated with movement across food gradients and corresponding feeding rhythms, indicating a trade-off between stickleback avoidance and feeding opportunity.

The adaptive benefit of vertical migration

Skistodiaptomus oregonensis vertically migrate only in the two lakes containing pelagic sticklebacks (Kennedy and Paxton; Table 1), consistent with the hypothesis that the ultimate selective force for *S. oregonensis* vertical migration is avoidance of stickleback predation. If juvenile sockeye predation was the selective force driving vertical migration, migrations would be expected in Great Central Lake, where juvenile sockeye density is more than twice that of Kennedy Lake, and migrations would not be expected in Paxton Lake where there are no juvenile sockeye (Table 1). The foraging efficiency hypothesis is not supported since food abundance nor food distribution distinguish lakes where migration occurs from those where migration does not occur. Under the bioenergetic hypothesis, temperature profiles in the two classes of lakes should differ to cause a temperature-dependent bioenergetic advantage for vertical migration only in the lakes where migration occurs. However, temperatures regimes are similar in all four lakes (Table 1, Figs. 2–4). Although the thermal advantage hypothesis may explain upward movement of migratory *S. oregonensis* to warmer water at night, it does not explain the deeper daytime distribution that distinguishes the behaviour of migratory and nonmigratory populations.

No other abiotic characteristics examined differ between the lakes consistent with differences in vertical migration of *S. oregonensis*. Neither light extinction nor pH values distinguish the lakes where *S. oregonensis* migrate from those where they do not. *Skistodiaptomus oregonensis* migrate in large and deep Kennedy Lake as well as in small and shallow Paxton Lake, and nonmigratory *S. oregonensis* are also found in both large and small lakes.

Evidence has accumulated for predator avoidance as the selective force driving vertical migration in many zooplankton species (e.g., Bollens et al. 1994; Neill 1992; Ohman 1990). Interlake comparisons demonstrating a positive relationship between migration and predation risk exist for *Cyclops abyssorum* (Gliwicz 1986) and *Diaptomus kenai* (Neill 1992). Schmidt et al. (1994) found greater migration of *Cyclops* sp. and *Diaptomus* sp. in lakes with higher predation risk. *Skistodiaptomus oregonensis* in McCargo Lake migrate extensively

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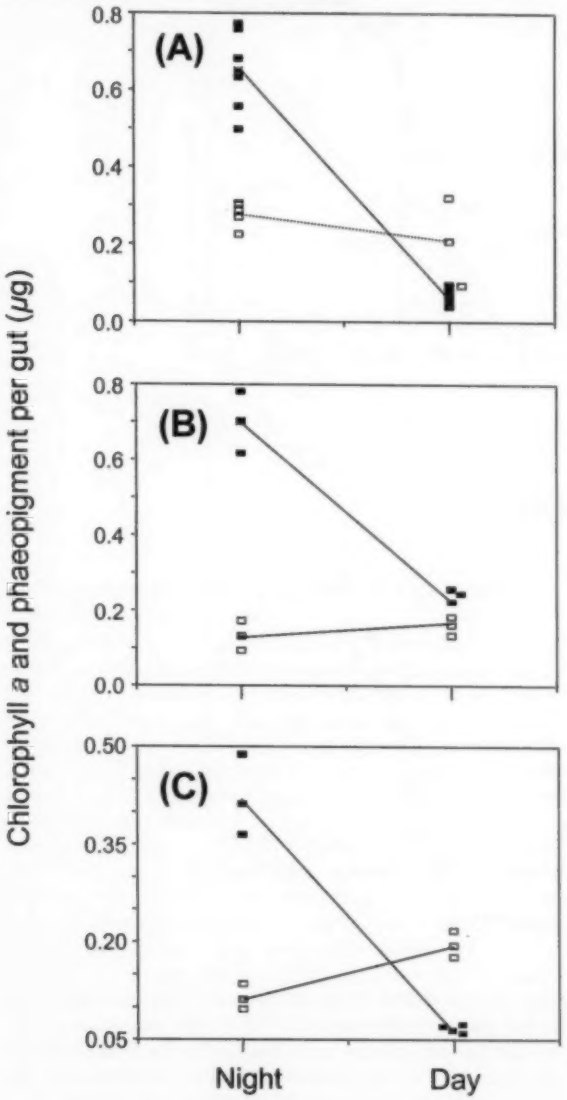
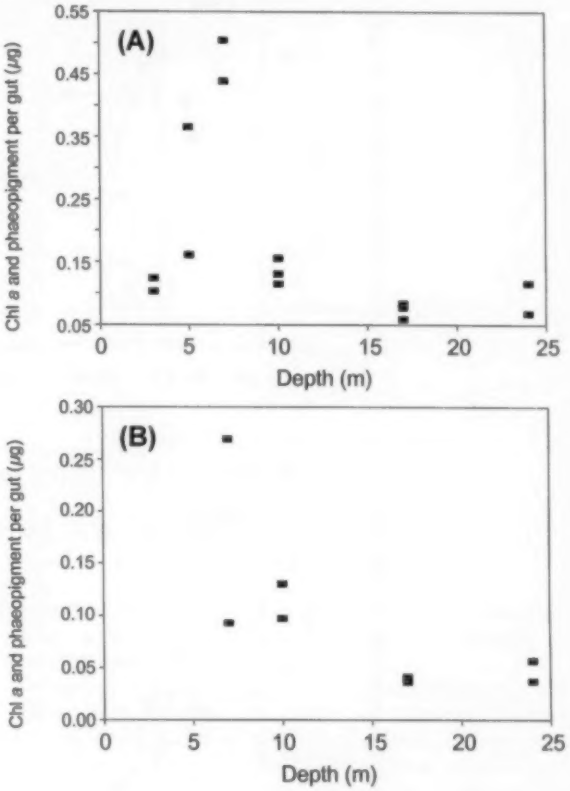
Fig. 7. Day versus night gut pigments in *S. oregonensis* in Kennedy Lake (solid squares) and Great Central Lake (open squares) on May 11–13, 1993 (A), June 22–23, 1993 (B), and July 15–16, 1993 (C). Each point represents the mean of 10 mature individuals. Lines join grand mean at each time within each lake.



in contrast to weakly or not at all in Lime Lake in western New York State. However information on predation risk in these lakes is lacking (Stewart and Sutherland 1993).

Within populations, many studies show seasonal onset, or changes, in the intensity of zooplankton migration that correspond to changes in predation risk. Examples include *Acartia hudsonica* (Bollens et al. 1992), *Diaptomus sanguineus* (De Stasio 1993), *Cyclops abyssorum*, *Mesocyclops* sp., *Eudiaptomus gracilis*, *Daphnia hyalina*, and *Bosmina* sp. (Stich 1989).

Fig. 8. Concentration of gut pigments in *S. oregonensis* versus depth captured during daytime in Kennedy Lake on June 23, 1993 (A), and July 16, 1993 (B). Each point represents the mean of 10 individuals.



Stickleback predation pressure

The hypothesis that stickleback predation drives vertical migration by *S. oregonensis* in Kennedy and Paxton lakes requires that pelagic stickleback present a significant predation risk. O'Neill and Hyatt (1987) demonstrated that sticklebacks in Kennedy Lake prefer copepods, including *S. oregonensis*, and stickleback in their lake enclosures were strongly selective of larger prey. Mature *S. oregonensis*, ranging from 800 to 1200 μm in total length, are the largest zooplankton species in Kennedy and Paxton Lake, with the exception of *Neomysis mercedis* (in Kennedy) and *Chaoborus* sp. (in Paxton). *Neomysis mercedis* and *Chaoborus* are themselves strong vertical migrators that are deep during the day and, thus, remain unavailable to stickleback.

Size-selective predation may cause vertical migration in the larger individuals within a prey species but not in the smaller individuals (e.g., Angeli et al. 1995). The total distance of vertical migration by *S. oregonensis* did, indeed, decrease with size for metasome length-classes less than about 450 μm (625 μm total length; Fig. 7). In comparison, O'Neill and Hyatt (1987) found that size-selective stickleback predation cropped the mean total length of zooplankton from 450–550 μm to 190–330 μm in enclosure experiments in Kennedy

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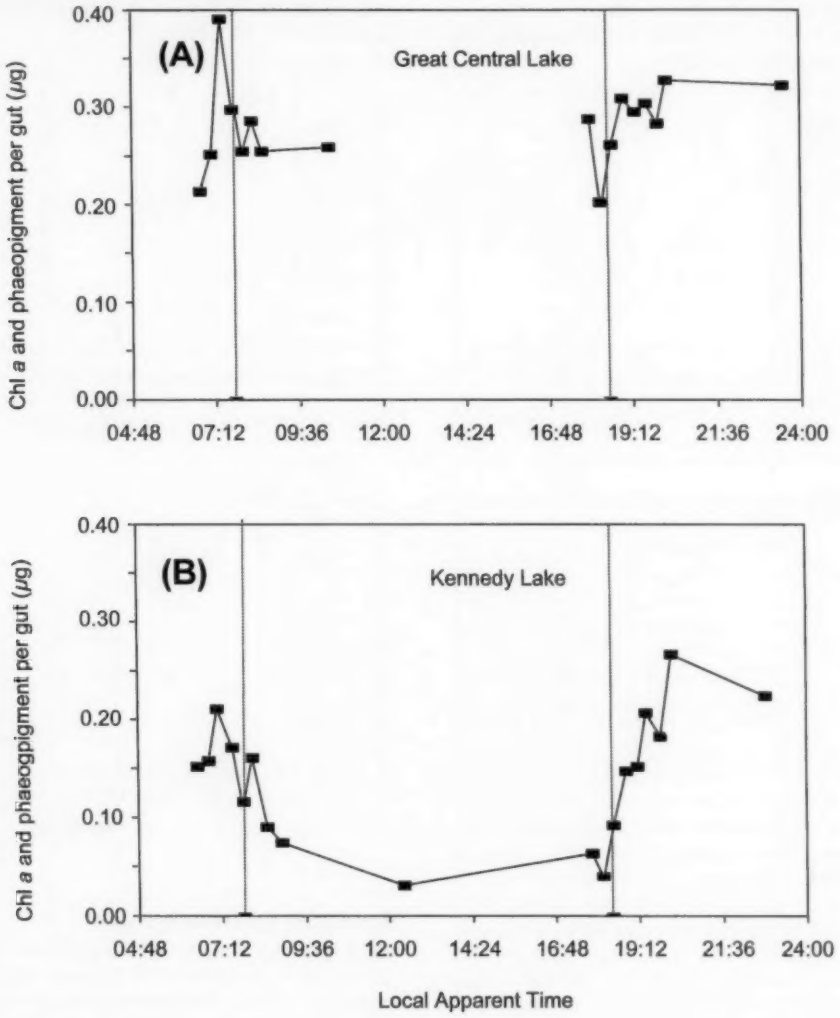
Fig. 9. Change in the concentration of pigments in the guts of *S. oregonensis* at dawn and dusk in Great Central Lake (A) and Kennedy Lake (B), October 17–20, 1993. Other details are as in Fig. 8.



Lake. Thus, we might expect that below this size range (190–330 μm), the strength of the vertical migration in *S. oregonensis* would decline.

Juvenile sockeye predation pressure

Our conclusion that abundant juvenile sockeye in the study lakes do not drive vertical migration by *S. oregonensis* while the stickleback do contrasts with the observation that the effect of size-selective cropping by juvenile sockeye and stickleback in Kennedy Lake enclosures was similar. Juvenile sockeye in Lake Washington also select larger zooplankton prey (Eggers 1982). In Alaskan, diaptomids have been observed to migrate in lakes containing high densities of juvenile sockeye but not in others where densities were low (Schmidt et al. 1994).

These apparent contradictions relate to differences in the timing of the predation risk from the two predators in our study lakes. The available evidence indicates that stickleback are diurnal predators (Manzer 1976). If so, they may exert predation pressure in surface waters that selects for vertical migration of *S. oregonensis* away from surface waters during the day. Juvenile sockeye are primarily crepuscular feeders (Barraclough and Robinson 1972; McDonald 1973; Narver 1970), and thus, the timing of *S. oregonensis* migration into and out of surface waters at dawn and dusk is critical to determine if predation by juvenile sockeye may be driving the vertical migration. The effect of vertical migration by *S. oregonensis* on its availability to both stickleback and juvenile sockeye has potential implications for the resource competition that may exist between these two planktivores in many coastal lakes (O'Neill and Hyatt 1987). The temporal–spatial pattern of predation by both sockeye and stickleback relative to the vertical migration of *S. oregonensis* is examined in further detail in Ghan et al. (1998).

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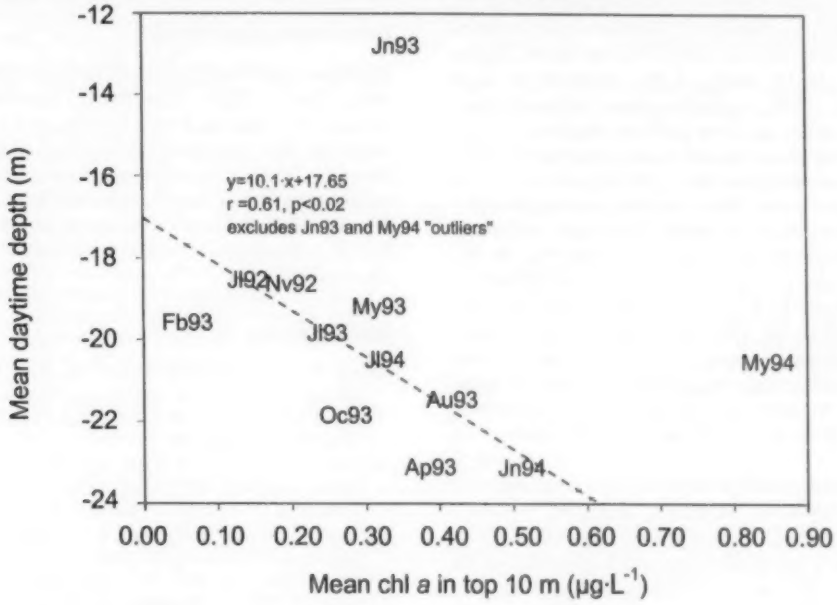
Fig. 10. Weighted mean daytime depth of *S. oregonensis* in Kennedy Lake versus mean concentration of chlorophyll *a* of the 3–50 µm size fraction of phytoplankton in the top 10 m. Dates (month/year) indicated for each sample point.



Vertical migration, feeding rhythms, and the feeding opportunity cost

Williamson et al. (1996) challenged a "paradigm of vertical migration theory" that vertical migration downward during the day results in a feeding opportunity cost, because food is most dense in surface waters. They demonstrated that *S. oregonensis* and *Daphnia pulicaria* both migrate down to metalimnetic waters where there is more food and up to epilimnetic waters with less food available at night. Under constant laboratory conditions, ingestion and reproduction was greater for both species when held in aquaria containing the deeper metalimnetic water versus the epilimnetic water. In contrast, *S. oregonensis* in Kennedy and Paxton lakes migrated from shallower water at night where food was more dense to deeper water during the day where food was less dense.

In Kennedy Lake, feeding rhythms did correspond with this vertical movement across a gradient of food density indicating a feeding opportunity cost. The absence of a feeding rhythm in the nonmigratory *S. oregonensis* population in Great Central Lake, and the fact that, on some dates, some Kennedy Lake *S. oregonensis* remained at the surface and fed during the day, are strong evidence that vertical migration was the cause of the feeding rhythm. Similarly, Angeli et al. (1995) showed that large *Daphnia* migrated across a vertical food gradient and displayed a feeding rhythm, while small *Daphnia* and mature *Eudiaptomus* only migrated within a zone of homogenous food and did not display a feeding rhythm. Gibbons (1992) found that an offshore population of *Sagitta serratodentata tasmanica* that migrated across a food density gradient and displayed a feeding rhythm, while an inshore population of the same species migrated within a homogenous food zone and fed continuously. *Calanus finmarchicus* (Gauld 1953; Simard et al. 1985), *Calanus pacificus* (Hassett and Landry 1988), and *Calanus hyperboreus* (Head et al. 1985) have also been observed to migrate across food density gradients and display diel feeding rhythms.

Contrary evidence suggests that vertical migration, and feeding may sometimes be controlled separately. Feeding rhythms in the absence of vertical migration are reported (e.g., Morales et al. 1993; Tang et al. 1994). Also, the timing of feeding rhythms does not always correspond with vertical migration movements (e.g., Atkinson et al. 1992*b*; Dagg et al. 1989; Tang et al. 1994). Feeding rhythms are known where migration depth ranges within a homogenous food distribution (e.g., Atkinson et al. 1992*a*; Cervetto et al. 1995), although a lack of feeding rhythm under these same conditions also occurs (e.g., Mourelatos et al. 1989).

Perhaps, both vertical migration and the cessation of daytime feeding are separate, complementary strategies that reduce daytime predation risk and co-occur in environments where predation risk is high. The cessation of daytime feeding may decrease predation risk by reducing movement and gut pigmentation that attract predators (Bollens and Stearns 1992). Further observations are required to test this hypothesis.

The existence of feeding rhythms does not necessarily imply that there is a decrease in net food intake over 24 h. Migrators that feed less during the day may compensate with increased night time food intake in such a way that total intake over the diurnal period is equal in migrators and nonmigrators (Angeli et al. 1995). Higher night gut pigment value in migrating *S. oregonensis* in Kennedy Lake relative to both night and day values in Great Central Lake in May, June, and July of 1993 (Fig. 8) suggest that they may compensate for lower daytime feeding during the day by feeding more at night, although this clearly does not occur in October (Fig. 10). However, lower gut fluorescence in Great Central Lake *S. oregonensis*

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may also result from the ingestion of nonfluorescing food types or because there is less available food.

To evaluate the effect of diurnal feeding rhythms on net daily intake requires knowledge of digestion and satiation rates. Bimodal feeding rhythms with dusk and dawn feeding maxima and low rates of feeding in the middle of the night (e.g., Atkinson et al. 1992*b*), suggests satiation after dusk feeding may last until dawn. In Kennedy Lake, however, *S. oregonensis* gut fluorescence measured near midnight on October 17, 1993 (Fig. 10), is nearly as high as the highest mean value recorded post-dusk on that date. Furthermore, large differences in gut fluorescence are detectable in samples taken near midnight when compared with daytime samples (Fig. 8). Reported gut passage times for zooplankton are rapid: 38 min for *Acartia tonsa* (Cervetto et al. 1995) and 100 min for *Metridia* spp. and *Pleuromamma* spp. (Morales et al. 1993). Given such rapid gut passage times, *S. oregonensis* likely need to feed continuously to maintain high gut pigments through the night. This suggests they would not remain satiated during the long day period away from more concentrated surface food resources.

Johnsen and Jakobsen (1987) showed a significant decrease in the daytime depth of vertically migrating *Daphnia longispina* in response to an experimentally depleted food supply in enclosures and argued that this was a reflection of the optimal strategy to balance a trade-off between feeding and predator avoidance. The mean daytime depth of *S. oregonensis* in Kennedy Lake also shows a tendency to decrease as food supply in the top 10 m decreased. Although these results must be interpreted with caution, as sample size is low and outliers were removed, they do provide some evidence for a feeding opportunity cost associated with vertical migration.

Summary

The hypothesis that vertical migration by *S. oregonensis* is driven by stickleback predation is supported by our comparison of four lakes with contrasting predator populations. Alternative hypotheses, including avoidance of juvenile sockeye, increased foraging and bioenergetic efficiency, and the interaction of foraging and bioenergetic efficiency are not consistent with our between lake observations. The stickleback avoidance hypothesis has also been supported by enclosure experiments, which indicate that stickleback do exert predation pressure on the same size-classes of *S. oregonensis* that vertically migrate in Kennedy Lake (O'Neill and Hyatt 1987). Juvenile sockeye also exert strong predation pressure but appear not to drive vertical migration, perhaps because they are crepuscular feeders rather than diurnal feeders.

Vertical migration appears to result in feeding opportunity costs. Phytoplankton food was less concentrated in the deep habitat where *S. oregonensis* resided during the day. Gut pigment concentrations were lower during the day than at night in migratory Kennedy Lake *S. oregonensis*, while gut pigment concentrations in nonmigratory *S. oregonensis* from Great Central Lake did not differ between day and night. Within Kennedy Lake, *S. oregonensis* near the surface during the day contained more gut pigments than did individuals in deep water. A decrease in mean depth of *S. oregonensis* as food abundance decreased also suggests a feeding opportunity cost. The trade-off between predator avoidance and feeding in vertical migration explains the persistence of both migratory and nonmigratory behaviour in different populations of *S. oregonensis* subject to differing selective pressures.

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References

Angeli, N., Pinel-Alloul, B., Balvay, G., and Menard, I. 1995. Diel patterns of feeding and vertical migration in daphnids and diaptomids during the clear water phase in Lake Geneva (France). Hydrobiologia, **300/301**: 163–184.

Atkinson, A., Ward, P., Williams, R., and Poulet, S.A. 1992*a*. Diel vertical migration and feeding of copepods at an oceanic site near South Georgia. Mar. Biol. **113**: 583–593.

Atkinson, A., Ward, P., Williams, R., and Poulet, S.A. 1992*b*. Feeding rates and diel vertical migration of copepods near South Georgia: comparison of shelf and oceanic sites. Mar. Biol. **114**: 49–56.

Barraclough, W.E., and Robinson, D. 1972. The fertilization of Great Central Lake III. Effect on juvenile sockeye salmon. Fish. Bull. U.S. **70**: 37–48.

Bollens, S.M., and Stearns, D.E. 1992. Predator-induced changes in the diel feeding cycle of a planktonic copepod. J. Exp. Mar. Biol. Ecol. **156**: 179–16.

Bollens, S.M., Frost, B.W., Thoreson, D.S., and Watts, S.J. 1992. Diel vertical migration in zooplankton: field evidence in support of the predator avoidance hypothesis. Hydrobiologia, **234**: 33–39.

Bollens, S.B., Frost, B.W., and Cordell, J.R. 1994. Chemical, mechanical and visual cues in the vertical migration behavior of the marine planktonic copepod *Acartia hudsonica*. J. Plankton Res. **16**: 555–564.

Cervetto, G., Pagano, M., and Gaudy, R. 1995. Feeding behaviour and migration in a natural population of the copepod *Acartia tonsa*. Hydrobiologia, **300/301**: 237–248.

Dagg, M.J., Frost, B.W., and Walser, W.E.J. 1989. Copepod diel migration, feeding, and vertical flux of pheopigments. Limnol. Oceanogr. **34**: 1062–1071.

De Stasio, B.T.J. 1993. Diel vertical migration and horizontal migration by zooplankton: population budgets and the diurnal deficit. Bull. Mar. Sci. **53**: 44–64.

Eggers, D.M. 1982. Planktivore preference by prey size. Ecology, **63**: 381–390.

Enright, J.T. 1977. Diurnal vertical migration: adaptive significance and timing. Part 1. Selective advantage: a metabolic model. Limnol. Oceanogr. **22**: 856–872.

Enright, J.T., and Honegger, H.-W. 1977. Diurnal vertical migration: adaptive significance and timing. Part 2. Test of the model: details of timing. Limnol. Oceanogr. **22**: 873–886.

Gauld, D.T. 1953. Diurnal variations in the grazing of planktonic copepods. J. Mar. Biol. Assoc. U.K. **31**: 461–474.

Ghan, D., McPhail, J.D., and Hyatt, K. 1998. The timing and extent of vertical migration by the freshwater copepod *Skistodiaptomus oregonensis* relative to the temporal–spatial distribution of predation risk. Can. J. Fish. Aquat. Sci. **55**. This issue.

Gibbons, M.J. 1992. Diel feeding and vertical migration of *Sagitta serratodentata* Krohn *tasmanica* Thomson (Chaetognatha) in the southern Benguela. J. Plankton Res. **14**: 249–259.

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Gliwicz, M.Z. 1986. Predation and the evolution of vertical migration in zooplankton. Nature (London), **320**: 746–748.

Hartmann, H.J., Taleb, H., Aleya, L., and Lair, N. 1993. Predation on ciliates by the suspension-feeding calanoid copepod *Acanthodiaptomus denticornis*. Can. J. Fish. Aquat. Sci. **50**: 1382–1393.

Hassett, R.P., and Landry, M.R. 1988. Short-term changes in feeding and digestion by the copepod *Calanus pacificus*. Mar. Biol. **99**: 63–74.

Head, E.J.H., Harris, L., and Abou Debs, C. 1985. Effect of daylength and food concentration on *in situ* diurnal feeding rhythms in Arctic copepods. Mar. Ecol. Prog. Ser. **24**: 281–288.

Hyatt, K.D., and Stockner, J.G. 1985. Responses of sockeye salmon (*Oncorhychus nerka*) to fertilization of British Columbia coastal lakes. Can. J. Fish. Aquat. Sci. **42**: 320–331.

Hyatt, K.D., Rutherford, D., Gjernes, T., Rankin, P., and Cone, T. 1984. Lake enrichment program: juvenile sockeye unit survey guidlines. Department of Fisheries and Oceans, Nanaimo, B.C.

Johnsen, G.H., and Jakobsen, P.J. 1987. The effect of food limitation on vertical migration in *Daphnia longispina*. Limnol. Oceanogr. **32**: 873–860.

Jonsson, P.R. 1989. Vertical distribution of planktonic ciliates—an experimental analysis of swimming behaviour. Mar. Ecol. Prog. Ser. **52**: 39–53.

Kerfoot, W.C. 1985. Adaptive value of vertical migration: comments on the predation hypothesis and some alternatives. Contrib. Mar. Sci. **27**: 91–113.

Ketelaars, H.A.M., Wagenvoort, A.J., and Reglindis, F.H. 1995. Life history characteristics and distribution of *Bythotrephes longimanus* Leydig (Crustacea, Onychopoda) in the Biesbosch reservoirs. Hydrobiologia, **307**: 239–251.

Lampert, W. 1989. The adaptive significance of diel vertical migration in zooplankton. Funct. Ecol. **3**: 21–27.

Lampert, W. 1993. Ultimate causes of diel vertical migration of zooplankton: new evidence for the predator avoidance hypothesis. Ergeb. Limnol. **39**: 79–88.

Manzer, J.I. 1976. Distribution, food, and feeding of the threespine stickleback, *Gasterosteus aculeatus*, in Great Central Lake, Vancouver Island, with comments on competition for food with juvenile sockeye salmon, *Oncorhynchus nerka*. Fish. Bull. U.S. **74**: 647–668.

McDonald, J. 1973. Diel vertical movements and feeding habits of underyearling sockeye salmon (*Oncorhynchus nerka*), at Babine Lake, B.C. Fisheries Research Board of Canada, Nanaimo, B.C.

McLaren, I.A. 1963. Effects of temperature on growth of zooplankton and the adaptive value of vertical migration. J. Fish. Res. Board Can. **20**: 685–727.

McPhail, J.D. 1993. Ecology and evolution of sympatric sticklebacks (*Gasterosteus*): origin of species pairs. Can. J. Zool. **71**: 515–523.

McQueen, D.J. 1970. Grazing rates and food selection in *Diaptomus oregonensis* (Copepoda) from Marion Lake, British Columbia. J. Fish. Res. Board Can. **27**: 13–20.

Morales, C.E., Harris, R.P., Head, R.N., and Tranter, P.R.G. 1993. Copepod grazing in the oceanic northeast Atlantic during a 6 week drifting station: the contribution of size classes and vertical migrants. J. Plankton Res. **15**: 185–211.

Mourelatos, S., Rougier, C., and Pourriot, R. 1989. Diel patterns of zooplankton grazing in a shallow lake. J. Plankton Res. **11**: 1021–1035.

Narver, D.W. 1970. Diel vertical migration and feeding of underyearling sockeye salmon and the limnetic zooplankton in Babine Lake, British Columbia. J. Fish. Res. Board Can. **27**: 281–316.

Neill, W.E. 1992. Population variation in the ontogeny of predator-induced vertical migration of copepods. Nature (London), **356**: 54–57.

Ohman, M.D. 1990. The demographic benefits of diel vertical migration by zooplankton. Ecol. Monogr. **60**: 257–281.

O'Neill, S.M., and Hyatt, K.D. 1987. An experimental study of competition for food between sockeye salmon (*Oncorhynchus nerka*) and threespine sticklebacks (*Gasterosteus aculeatus*) in a British Columbia coastal lake. *In* Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. *Edited by* H.D. Smith, L. Margolis, and C.C. Wood. Can. Spec. Publ. Fish. Aquat. Sci. No. 96. pp. 143–160.

Osgood, K.E., and Frost, B.W. 1994. Ontogenetic diel vertical migration behaviors of the marine planktonic copepods *Calanus pacificus* and *Metridia lucens*. Mar. Ecol. Prog. Ser. **104**: 13–25.

Parsons, T.R., Takahashi, M., and Hargrave, B. 1984. Biological oceanographic processes. Pergamon Press, Toronto, Ont.

Pennak, R.W. 1989. Fresh-water invertebrates of the United States: Protozoa to Mollusca. John Wiley & Sons Inc, New York.

Ringelberg, J. 1993. Preface. Ergeb. Limnol. 39: *v–vii*.

Roff, J.C., and Hopcroft, R.R. 1986. High precision microcomputer based measuring system for ecological research. Can. J. Fish. Aquat. Sci. **43**: 2044–2048.

Schmidt, D.C., Koenings, J.P., and Kyle, G.B. 1994. Predator-induced changes in copepod vertical migration: explanations for decreased overwinter survival of sockeye salmon. *In* Theory and application in fish feeding ecology. Vol. 18. *Edited* by M. Duke. University of South Carolina Press, Columbia. pp. 187–209.

Simard, Y., Lacroix, G., and Legendre, L. 1985. In situ twilight grazing rhythm during diel vertical migrations of a scattering layer of *Calanus finmarchicus*. Limnol. Oceanogr. **30**: 598–606.

Stewart, K.M., and Sutherland, J.W. 1993. Zooplankton migrations in three lakes of western New York. Int. Rev. Gesamten Hydrobiol. **78**: 21–37.

Stich, H.B. 1989. Seasonal changes of diel vertical migrations of crustacean plankton in Lake Constance. Arch. Hydrobiol. Suppl. **83**: 355–405.

Stich, H.B., and Lampert, W. 1981. Predator evasion as an explanation of diurnal vertical migration by zooplankton. Nature (London), **293**: 396–398.

Tang, K.W., Chen, Q.C., and Wong, C.K. 1994. Diel vertical migration and gut pigment rhythm of *Paracalanus parvus, P. crassirostris, Acartia erythraea,* and *Eucalanus subcrassus* (Copepoda, Calanoida) in Tolo Harbour, Hong Kong. Hydrobiologia, **292/293**: 389–396.

Vanderploeg, H.A. 1990. Feeding mechanisms and particle selection in suspension-feeding zooplankton. *In* The biology of particles in aquatic systems. *Edited* by R.S. Wotton. CRC Press, Boca Raton, Fla. pp. 183–212.

Williamson, C.E., Sanders, R.W., Moeller, R.E., and Stutzman, P.L. 1996. Utilization of subsurface food resources for zooplankton reproduction: implications for diel vertical migration theory. Limnol. Oceanogr. **41**: 224–233.

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The temporal–spatial pattern of vertical migration by the freshwater copepod *Skistodiaptomus oregonensis* relative to predation risk

David Ghan, J.D. McPhail, and K.D. Hyatt

Abstract: *Skistodiaptomus oregonensis* vertical migration in Kennedy Lake and Paxton Lake may be an adaptation to avoid predation by threespine stickleback (*Gasterosteus aculeatus*). In Kennedy Lake, juvenile sockeye salmon (*Oncorhynchus nerka*) and the mysid *Neomysis mercedis* are also predators that potentially drive the vertical migration. A corollary of the hypothesis that predation selects for vertical migration is that the extent and timing of the vertical migration decreases predation risk. This corollary is tested for each of the potential predators. Laboratory experiments indicate that stickleback feeding rate decreases below 1.6 $\mu E \cdot s^{-1} \cdot m^{-2}$. In Kennedy and Paxton lakes, *S. oregonensis* occupied depths below this light intensity during the day. Furthermore, as *S. oregonensis* ascended at dusk and descended at dawn, they remained within light intensities that reduced stickleback predation rate. In Kennedy Lake, hydroacoustic data coupled with information in the literature on feeding behaviour of juvenile sockeye indicate that this species move to surface waters to feed before sunrise and after sunset. Vertically migrating *S. oregonensis* are near the surface during the twilight feeding periods of juvenile sockeye. The timing of *S. oregonensis* vertical migration also does not reduce the time it is in contact with the predator *N. mercedis*.

Résumé : La migration verticale de *Skistodiaptomus oregonensis* dans les lacs Kennedy et Paxton pourrait être une adaptation permettant d'éviter un prédateur, l'épinoche à trois épines (*Gasterosteus aculeatus*). Dans le lac Kennedy, deux autres espèces prédatrices, le saumon rouge (*Oncorhynchus nerka*) et le mysidacé *Neomysis mercedis* pourraient également être à l'origine du phénomène des migrations verticales. L'hypothèse selon laquelle la migration verticale est due à la prédation a notamment pour corollaire que l'ampleur de la migration et le moment où elle survient réduisent le risque de prédation. Nous avons testé ce corollaire pour chacune des espèces susceptibles de chasser *S. oregonensis*. Des expériences en laboratoire ont permis de déterminer que l'activité prédatrice de l'épinoche diminue lorsque l'intensité lumineuse est inférieure à 1,6 $\mu E \cdot s^{-1} \cdot m^{-2}$. Le jour, dans les lacs Kennedy et Paxton, *S. oregonensis* se trouve à des profondeurs où l'intensité lumineuse est inférieure à cette valeur. En outre, en montant vers la surface, au crépuscule, et en descendant en profondeur, à l'aube, il demeure dans des conditions d'intensité lumineuse réduisant l'activité prédatrice de l'épinoche. Si l'on en juge d'après les données d'hydroacoustique et les publications sur l'alimentation du saumon rouge, dans le lac Kennedy les saumons rouges juvéniles remontent vers les eaux de surface pour se nourrir avant le lever et après le coucher du soleil. Or, les populations de *S. oregonensis* qui migrent à la verticale se trouvent près de la surface de l'eau au crépuscule, lorsque les saumons juvéniles remontent se nourrir. Par ailleurs, le moment où *S. oregonensis* migre ne réduit pas la durée de son contact avec l'espèce prédatrice *N. mercedis*.
[Traduit par la Rédaction]

Introduction

It has been proposed that daytime vertical migration of zooplankton is a strategy to decrease risk from visual predators (Angeli et al. 1995; Bollens and Frost 1989; Mangel and Clarke 1988; Zaret and Suffern 1976). Our comparative study in four lakes (summarized in Table 1) suggested that vertical migration by the copepod *S. oregonensis* in two lakes is an adaptation to avoid predation by visually feeding threespine sticklebacks (*Gasterosteus aculeatus*) (Ghan et al. 1998).

Predation by juvenile sockeye salmon (*Oncorhynchus nerka*) does not appear to influence vertical migration; juvenile sockeye are absent in Paxton Lake where *S. oregonensis* migrated and are present in Hobiton and Great Central lakes, where *S. oregonensis* did migrate. This is surprising because juvenile sockeye and stickleback held in enclosures in Kennedy Lake were both size-selective plantivores with strong and similar impacts on the zooplankton community (O'Neill and Hyatt 1987) and because unusually high abundance levels of juvenile sockeye appear to have produced a shift in copepod behaviour from no migration to migration in Alaskan lakes (Schmidt et al. 1994).

Predation may select for vertical migration if vertical migration decreases predation risk. Differences in the diurnal timing of feeding of stickleback and juvenile sockeye may explain why only the former select for vertical migration in

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Table 1. Biological and physical conditions in four study lakes.

	Great Central	Hobiton	Paxton	Kennedy
Skistodiaptomus oregonensis migration	No	No	Yes	Yes
Pelagic stickleback density (no.·ha^{-1})[a]	0[b]	0[b]	Present[c]	957
Juvenile sockeye density (no.·ha^{-1})[a]	1356	775	0[c]	555
Zooplankton biomass (mg dry weight·m^{-3})	9	11	Unknown	5.4
Mean chl *a* 0–10 m (μg·mL^{-1})	0.291	0.289	1.7	0.339
Annual primary production (g C·m^{-2})	18.9	28.7	Unknown	16.5
Elevation (m)	82	15	61	4
Area (km^2)	51	3.6	0.162	64
Mean depth (m)	212	36	33	16
Light extinction	0.44	0.44	0.5	0.38
Compensation depth (m)	18.5	10.4	Unknown	12.3
Temperature (°C)[d]	18.4	17.8	Maximum 23	18.1
pH	7	6.8	Unknown	7.1

[a]Mean values for 10 annual estimates from 1986 to 1995 via hydroacoustic and trawl surveys in late fall to early winter (K. Hyatt, Fisheries and Oceans Canada, unpublished data). Consult Hyatt et al. (1984) and Hyatt and Stockner (1985) for detail on methods of survey and analysis, respectively.

[b]Although stickleback are present in both Great Central and Hobiton lakes, Fisheries and Oceans trawl surveys over more than a decade indicate their absence from open water.

[c]See McPhail (1993).

[d]Mean temperature June 1 and Sept. 30 at 1 m.

our study lakes. Observations in Kennedy Lake suggest that stickleback feed near the surface during the day. Stickleback have been seen feeding offshore in surface waters during the day in summer and fall and can be caught in minnow traps placed in this habitat during the day.

In contrast, diurnal hydroacoustic sampling of depth distribution, analyses of gut contents, and visual observations of surface feeding (Barraclough and Robinson 1972; Levy 1990; McDonald 1973; Narver 1970) indicate that juvenile sockeye are primarily crepuscular feeders that also vertically migrate (with the exception of glacially turbid lakes; Hyatt et al. 1989). Typically, juvenile sockeye remain in deep water during the day, and their feeding rate is low. They ascend toward the surface to feed during twilight (Barraclough and Robinson 1972). At night, they move to the thermocline. Dense schooling and the rarity of fresh food in gut samples indicate that the feeding rate is low at night. At dawn, sockeye may approach the surface and feed again before descending to depth for the day. Predation by juvenile sockeye may be a selective force for the migration of *S. oregonensis* only if the *S. oregonensis* migration is timed so that they avoid surface waters during the juvenile sockeye crepuscular feeding period.

In this paper, we investigate the effectiveness of vertical migration by *S. oregonensis* as a predator avoidance strategy. We consider whether the movement of *S. oregonensis* over the diurnal cycle cause them to occupy depths where light levels are low enough to reduce predation risk from stickleback and juvenile sockeye. Since the mysid *Neomysis mercedis*, an invertebrate predator, is also present in Kennedy Lake we consider how migration by *S. oregonensis* effects its vulnerability to this species as well.

Materials and methods

Stickleback feeding rate experiment

Sticklebacks were collected from Kennedy Lake in minnow traps on May 21, 1995, transported to the laboratory, and held in a 208-L holding tank illuminated by two 40-W Vita-Lite full-spectrum fluorescent lights. An automatic switch turned the lights off at sunset and on at sunrise. The stickleback were daily fed live zooplankton collected from Shirley Lake and (or) Marion Lake in the University of British Columbia Research Forest. Shirley Lake zooplankton consisted mainly of *Hesperodiaptomus kenai*, fourth-instar *Chaoborus trivittatus*, and *Aglaodiaptomus leptopus*. Marion Lake zooplankton consisted mainly of mature *S. oregonensis* (779 μm mean metasome length), *S. oregonensis* copepodites (410 μm mean metasome length), and a cyclopoid copepod (440 μm mean metasome length). Every 2 or 3 days, the stickleback were fed thawed *Tubifex* worms.

Twenty-four hours before the beginning of experimental trials for each day, 11 fish were transferred from the holding tank to a 56-L starvation tank. The experimental feeding unit consisted of an outer clear Plexiglas tank measuring 30 × 58 × 38 cm into which was placed a 27 × 51 × 32 cm inner tank constructed of clear Plexiglas vertical walls and a porous 100 μm Nitex mesh bottom. Lake water filtered through a 50-μm mesh was added to the feeding unit to a volume of 40 L in the inner tank. In preliminary trials, stickleback fed near the bottom on prey that were highly visible due to strong contrast created by reflection of the overhead light source by the Nitex mesh bottom. Nonreflective black araldite was placed over the mesh bottom to reduce reflection. With this addition, stickleback fed throughout the feeding unit. The exterior surface of the bottom and three of the four vertical walls of the outer tank were covered with brown packing paper over which was placed light impermeable black plastic. For observation, one of the larger vertical walls of the outer tank was left open, but covered from the outside by a large black cloth blind attached along the top edge of the open vertical wall by Velcro[7]. The observer, wearing dark clothing, sat motionless between the blind and the open wall. This allowed the observer to see into the tank and prevented background light from entering the tank through the open side wall.

Each day, for 6 days, 11 individual fish were fed at 11 different light intensity treatments. For each trial, Marion Lake zooplankton were added to the feeding unit and briefly mixed. Following this, a single fish was transferred from the starvation tank into the inner tank of the feeding unit. A sheet of Plexiglas was placed over the top of the experimental chamber and 1–11 sheets of grey, plastic Permascreen light filters were placed over the Plexiglas sheet to vary light intensity. All fish commenced feeding within 2–10 min of placement in the

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feeding unit. Once feeding behaviour had begun, the number of feeding strikes were recorded for 15 min. The fish was then removed, anaesthetized, killed in 95% ethanol, and then fixed in 4% formaldehyde. Zooplankton remaining in the feeding unit were collected by removing the araldite sheet from the bottom of the inner tank, lifting the mesh-bottomed feeding unit out of the outer tank, and rinsing the contents into a jar of 4% sugared formaldehyde.

In the laboratory, sticklebacks were dissected to ennumerate the number of *S. oregonensis* and the total number of zooplankton per stomach. Natural log transformations were performed on these data and on the number of feeding strikes. A capture/strike ratio was calculated for each fish and subjected to an arcsine square-root transformation. The transformations were used to reduce heteroscedasticity. Least-square linear regressions were then performed using each transformed variable as a dependent against the natural log of light intensity as an independent variable.

To determine the utilization of the large *S. oregonensis* relative to other prey categories available in the feeding treatments the Vanderploeg and Scavia index of electivity (Vanderploeg and Scavia 1979) was used:

$$E_i = \frac{\frac{r_i}{p_i}}{\sum_i^n \frac{r_i}{p_i}}$$

where E_i is the electivity of prey type i, r_i is the relative proportion of prey type i in the diet, and p_i is the relative proportion of each prey type available. The index ranges in value from 0 to 1. A value of $1/n$ indicates neutral selection, values above $1/n$ indicate positive selection, and values below $1/n$ indicate negative selection.

Field measures of vertical movements of zooplankton, fish, and light intensity at dawn and dusk

Simultaneous field measures were taken in Kennedy Lake during October 1993, June 1994, and May 1995 to assess vertical movements of zooplankton, fish, and light intensity isoclines during dawn and dusk. In Paxton Lake, measures to assess vertical movements of zooplankton and light-intensity isoclines were collected in August of 1994.

To track the timing of vertical migration by *S. oregonensis* during dawn and dusk, time series of vertically stratified zooplankton tows were collected from three discrete depth intervals with a closable double-ringed Wisconsin-style 100-µm Nitex mesh plankton net (292 cm in length and with a 55 cm diameter opening). Depth intervals were 24–12, 12–5, and 5–0 m in Kennedy Lake. In Paxton Lake, depth intervals sampled were 12–9, 9–4, and 4–0 m. It was not possible to sample below 12 m in Paxton Lake, with a maximum depth of 15 m, because of the length of the sample net. The three depth strata were sampled in rapid succession, from deepest to shallowest, over approximately 8–12 min. A 20-min interval was maintained between the start of one set of stratified samples and the start of the next set. Immediately upon retrieval, samples were preserved in 4% sugared formaldehyde.

In the laboratory, all *S. oregonensis* larger than 800 µm total length were counted under a Wild M-5 microscope. The subsampling was conducted as described in Ghan et al. (1998). In each stratum, abundance was estimated as the number of *S. oregonensis* occurring under a 1-m surface area (see Ghan et al. 1998). During the sampling in October 1993, a number of *N. mercedis* were also captured in Kennedy Lake, and these were ennumerated in each stratum as well.

To determine the timing of dawn and dusk vertical movement of juvenile sockeye in Kennedy Lake, the depth distribution of fish targets were determined with a 100-W Furuno FM-22 200 kHz hydroacoustic sounder during the intervals between each set of vertical zooplankton hauls described above. The sounder was mounted on a hydroplane lashed into position at 1 m depth alongside a boat moving at approximately 0.5–1.0 $m \cdot s^{-1}$ (see Hyatt et al. 1984 for further details). The time varied gain circuit, which controls for spreading and attenuation losses of the acoustic signal with distance, was inoperative on the sounder. This likely resulted in a depth-dependent bias in the estimated density of targets, but the data still provide a measure of the movement of targets across depth over time. Fish targets on the echosounder traces were counted to determine the mean number of fish targets per second in each stratum during each time interval.

Routine hydroacoustic and trawl surveys conducted by Fisheries and Oceans Canada indicate that offshore fish populations in Kennedy Lake consist almost exclusively of juvenile sockeye and stickleback. Our interpretation of vertical movement of juvenile sockeye from hydroacoustic measurements assumes that stickleback remain near the surface both day and night and that fish targets moving upward at dusk and downward at dawn are juvenile sockeye. Several observations justify this assumption. At night, routine trawl surveys in Kennedy Lake consistently indicate that stickleback remain in the top 15 m. In offshore surface waters during the day in Kennedy Lake, stickleback have been observed feeding and have been caught in minnow traps. Daytime SCUBA observations during enclosure studies in Kennedy Lake (O'Neill and Hyatt 1987) revealed that stickleback were active throughout the enclosure and spent much time foraging at the surface and along the sides of the enclosure at very shallow depths. The sockeye, in contrast, stayed close to the bottom of the 5-m enclosures.

Light extinction was determined near midday on each sample date by measuring light intensity at the surface and at 1-m depth intervals with a LI-COR 186A light meter. Light intensity at depth is given by

$$I_z = I_0 e^{-kz}$$

where I_z is the light extinction at depth z, I_0 is the light intensity at the surface, and k is the light extinction coefficient. This equation was rearranged to

$$\ln I_0 - \ln I_z = kz$$

and a least squares regression was fit to the field measurements of I_0, I_z, and z to determine the light extinction coefficient, k. This estimate of k was used to calculate light-intensity depth profiles during dawn and dusk sampling from measurements of light intensity at the surface (I_0). This method assumes that the light extinction coefficient does not change as light intensity changes over the dawn and dusk period. Levy (1989, fig. 5-5) demonstrated that k did not change during crepuscular periods in Cultus Lake and Great Central Lake, British Columbia.

Results

Stickleback feeding rate experiments

The mean density of zooplankton in the experimental treatments was 26.0·L^{-1} (range 18.8–36.7·L^{-1}). Densities did not differ among light intensity treatments (ANOVA, $F = 0.19$, $P < 0.9967$, treatment df = 10, error df = 55). Analyses of variance indicated no significant differences in the densities of the six major prey categories, which included cyclopoid copepods, large *S. oregonensis*, small *S. oregonensis*, *Bosmina* sp., large cladocerans, and small cladocerans ($P >$ F ranged from 0.96 to 1.00 for the six tests). Within each day, the total density as well as the proportion of each prey type in the experimental tanks were approximately equal across treatments (values for treatments on day 2 shown in Fig. 1). The daily means ranged from 21.6–31.8·L^{-1}, and there were significant differences in total densities among days (ANOVA, $F = 55.31$, $P < 0.0001$, treatment df = 5, error df = 60).

Experimental zooplankton densities were four to five times higher than the 6.2·L^{-1} (May 1995) and 6.4·L^{-1} (October 1993) estimated from the highest densities in vertically stratifed

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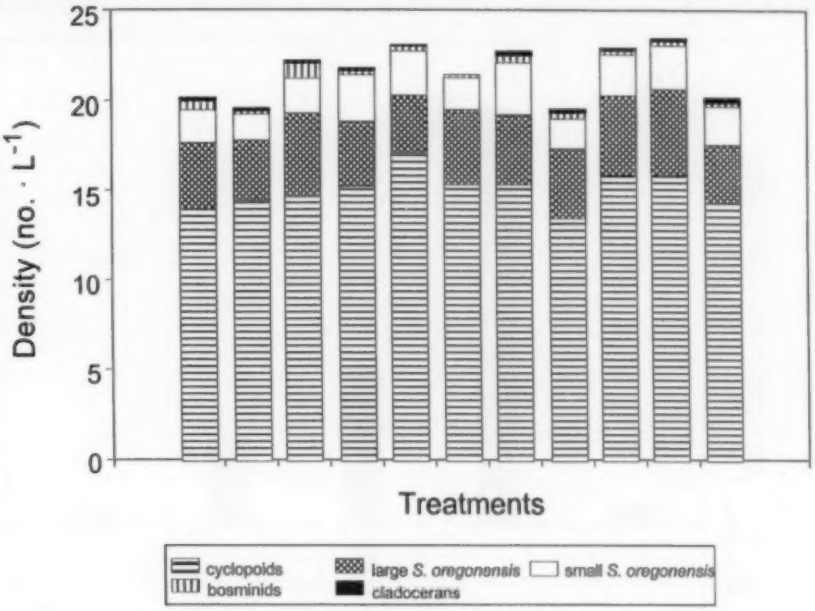
Fig. 1. Total densities of zooplankton in 11 experimental tank treatments broken down by taxa or size categories on experiment day 2.



zooplankton samples in Kennedy Lake. However, the relative proportions of the zooplankton taxa present (Fig. 2) and the sizes of these taxa (Fig. 3) are similar in the experimental treatments and in Kennedy Lake.

In the experiment, the number of *S. oregonensis* (Fig. 3A) and the total number of prey per stickleback stomach, the number of strikes, and the capture/strike ratio all increase significantly with light intensity over a light intensity range of 0.1–1.6 $\mu E \cdot s^{-1} \cdot m^{-2}$. After a light intensity of 1.6 $\mu E \cdot s^{-1} \cdot m^{-2}$ is reached there is no further significant light effect (Table 2).

At all light levels, large *S. oregonensis* are positively selected by most of the stickleback in these trials (Fig. 3B). The rate at which *S. oregonensis* are eaten is lowest at the two lowest light level treatments used in this experiment. Thus, the mean number of *S. oregonensis* per fish at the two lowest light levels was 1.45 ($n = 11$) compared with 23.42 ($n = 23$) at light levels above 1.6 $\mu E \cdot s^{-1} \cdot m^{-2}$.

Timing of *S. oregonensis* vertical migration in relation to stickleback feeding rate

Figures 4 and 5 plot the changes in the vertical distribution of *S. oregonensis* at dawn and dusk in Kennedy and Paxton lakes relative to the 1.6 µE isolume and the 0.1 µE isolume. Based on our experiments, these light levels are defined as the maximum (MFRT) and the near-zero feeding rate thresholds (FRT) for stickleback. Before sunrise on May 20, 1995 (Fig. 4A), light levels were below FRT at the surface and *S. oregonensis* were mainly located between 5 and 12 m. Most *S. oregonensis* followed the FRT isolume as it moved first into the 5–12 m stratum and later into the 12–24 m stratum. Most individuals were below the MFRT isolume throughout. At dusk on the same date (Fig. 4B), almost all *S. oregonensis* remained below 12 m until the FRT isolume rose above this depth and, again, most individuals remained below MFRT throughout the sample period. Similar patterns were also observed at dawn and dusk on June 24, 1994.

Assuming Paxton Lake sticklebacks share the same visual feeding thresholds, vertical migration in Paxton Lake *S. oregonensis* on August 19, 1994, also appeared to be timed to remain below the MFRT, and the data are consistent with the notion that most individuals remained below the FRT isolume (Fig. 5). During daylight hours, the FRT isolume was located at or just below 12 m, and low numbers of *S. oregonensis* sampled indicate most were also below 12 m and inaccessible to the net samples. This explains both the decrease in *S. oregonensis* caught after dawn, as the FRT isolume shifts to below the 9–12 m stratum, and the low numbers of *S. oregonensis* above 12 m at 18:29 followed by a sudden increase in numbers in the 9–12 m stratum at 18:49 just as the FRT isolume rises above 12 m (Fig. 5B).

The measured daytime depth distribution of *S. oregonensis* in Kennedy Lake indicate that the majority occupied depths where light intensities reduced stickleback feeding rate. Discrete samples at 1-, 3-, 5-, 7-, 10-, 17-, and 24-m intervals showed highest abundances of *S. oregonensis* at 17 or 24 m with few at 10 m or above (Ghan et al. 1998). The stratified vertical samples indicate *S. oregonensis* were below the 12-m depth as dusk sampling began and dawn sampling ended. In Kennedy Lake, during full sunlight (2000 $\mu E \cdot s^{-1} \cdot m^{-2}$), the MFRT light intensity is estimated to be at 16.9 m and FRT light intensity, at 23.8 m (using the extinction coefficient of 0.401 measured in June of 1994). Under cloudy conditions (1000 $\mu E \cdot s^{-1} \cdot m^{-2}$), MFRT is estimated to be at 15.2 m and FRT, at 22.1 m.

Timing of *S. oregonensis* vertical migration relative to sockeye vertical migrations

Several studies indicate that the timing of vertical migration

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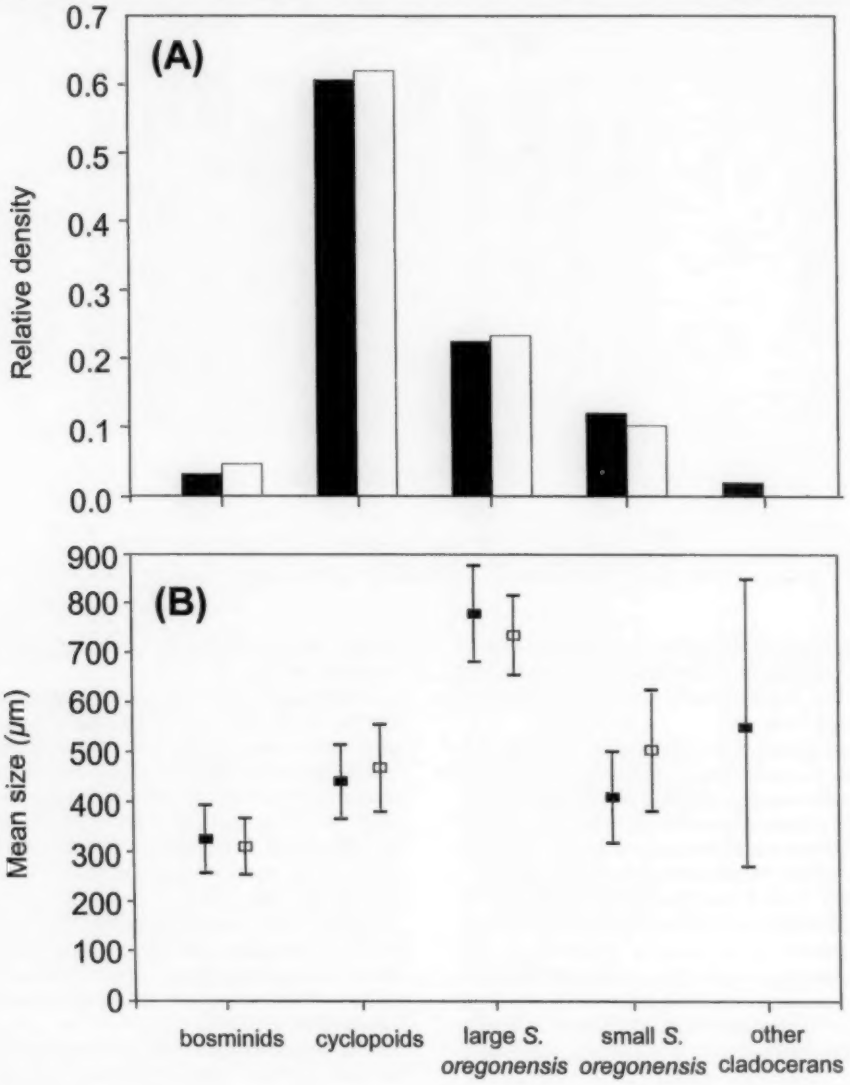
Fig. 2. A comparison of the relative density of prey types (A) and size of prey types (B) in one of the experimental tanks (solid bars and solid squares) and in Kennedy Lake (open bars and open squares) on May 20, 1995. Prey in experimental tanks were acquired from Marion Lake.



and feeding of juvenile sockeye is consistent relative to sunrise and sunset (Fig. 6). In 11 of 13 instances, ascent begins within 30 min of sunset, and they arrive near the surface by about 15–20 min after sunset. They feed for about 20–40 min before descending to the thermocline. Less data is available for the dawn period, and the rise from the thermocline to the surface for feeding is harder to define. Nonetheless, the available information indicates that feeding starts and ends before sunrise. Depth isolumes for maximum, half maximum, and minumum feeding rate light intensities of juvenile sockeye over dawn and dusk in Kennedy Lake (Fig. 7) indicate that juvenile sockeye have the visual capacity to feed near the surface up to an hour after sunset and an hour before sunrise.

Skistodiaptomus oregonensis was vulnerable to postsunset surface feeding by juvenile sockeye. At dusk on October 19, 1993 (Fig. 8), some deepwater fish targets, inferred to be juvenile sockeye, rose to <12 m within 10–15 min after sunset, shortly after the arrival of *S. oregonensis* in the surface stratum. If juvenile sockeye feed as they ascend (Barraclough and Robinson 1972), *S. oregonensis* were also exposed to predation from 10 min before to 15 min after sunset when both *S. oregonensis* and juvenile sockeye were moving through the 5–12 m stratum. Similar results were obtained on June 24, 1994, and May 19, 1995.

At dawn on June 24, 1994 (Fig. 9), and May 19, 1995 (not shown), juvenile sockeye began descent within 20 min of sunrise. *Skistodiaptomus oregonensis* began to shift downward from the 5–12 to 12–24 m depth interval at about the same

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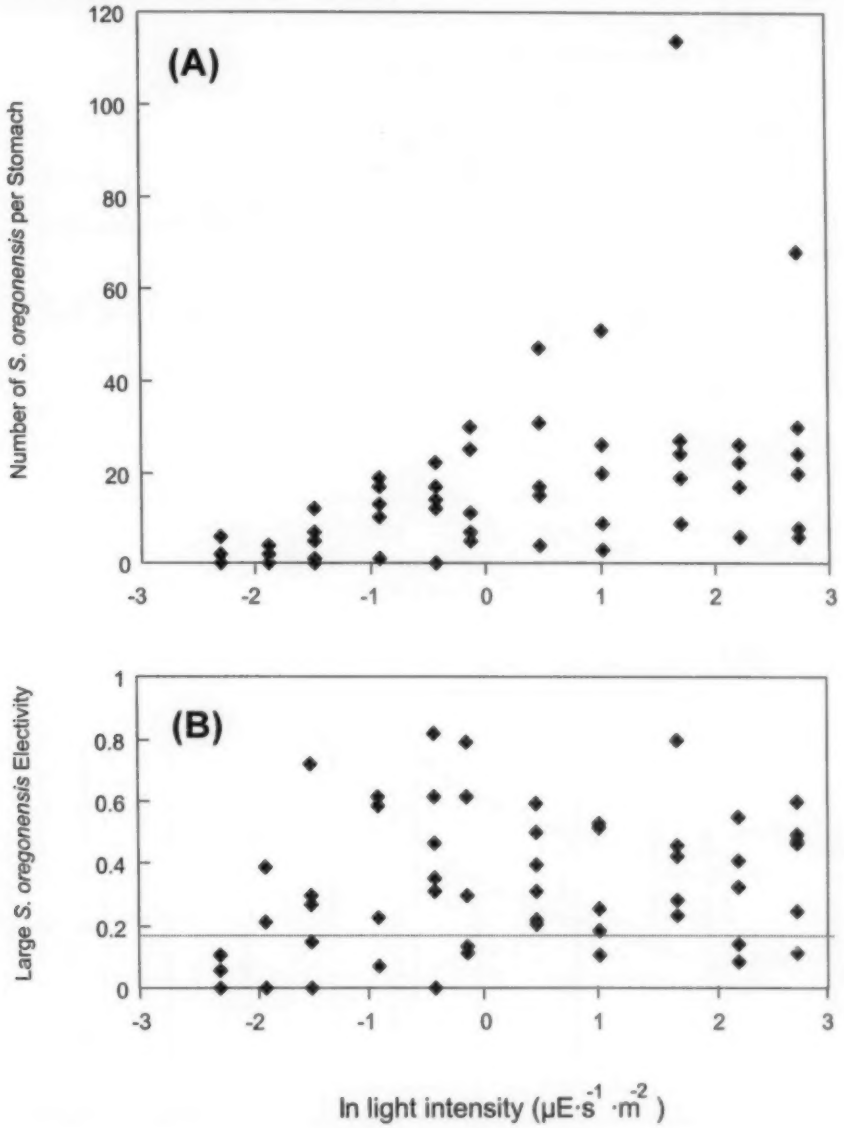
Fig. 3. Number of prey in the guts of stickleback stomachs (A) and corresponding Vanderploeg–Scavia indices of electivity for large *S. oregonensis* prey (B) at 11 different light intensities. Stickleback fed for 15 min. For electivities, values above dotted horizontal line show positive electivity, and values below this line show negative electivity.



time, or later, and therefore after the juvenile sockeye feeding period.

Timing of *S. oregonensis* vertical migration relative to *N. mercedis* vertical migrations

Neomysis mercedis, also a strong vertical migrator, was captured in abundance during the dusk sampling of October 1993. *Skistodiaptomus oregonensis* ascended to the 0–5 m stratum about 20–40 min earlier than *N. mercedis* (Fig. 10). Since *S. oregonensis* move upward well before the *N. mercedis* begin feeding near the surface, the timing of *S. oregonensis* movements did not effect their vulnerable to the *N. mercedis*.

Discussion

Extent and timing of *S. oregonensis* vertical migration in relation to stickleback feeding rate

As predicted by the stickleback avoidance hypothesis, *S. oregonensis* migrate deep enough during the day to decrease the feeding rate of stickleback. Furthermore, as *S. oregonensis* move up at dusk and down at dawn they closely track the threshold light intensity for stickleback feeding. If there is a feeding opportunity cost associated downward vertical migration, the optimal strategy may be to tolerate some predation risk. This may explain the position of some *S. oregonensis* at

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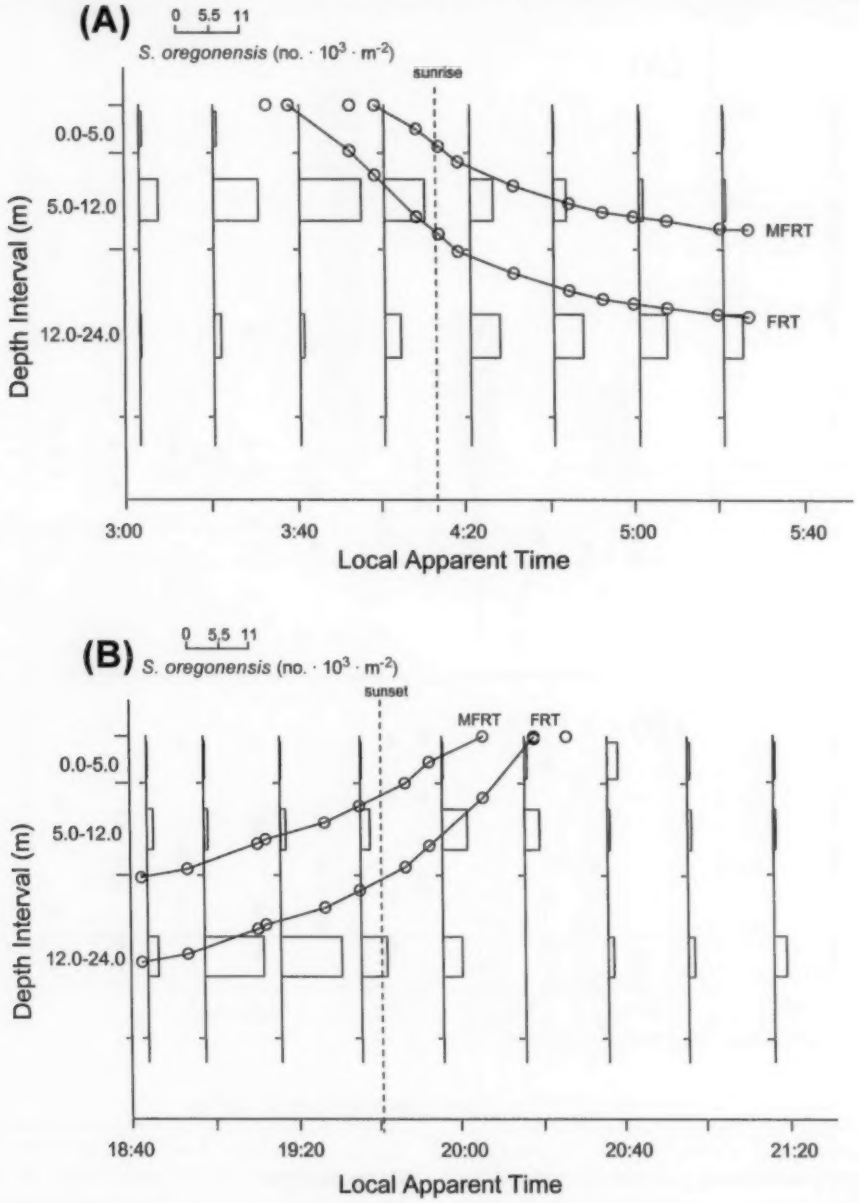
Fig. 4. Vertical migration of *S. oregonensis* relative to light thresholds for stickleback feeding in Kennedy Lake during dawn (A) and dusk (B) on May 20, 1995. Horizontal bar graphs represent total number of *S. oregonensis* under 1 m^2 surface in three depth strata. Curves represent depth isolumes for stickleback maximum feeding rate threshold (MFRT) and near-zero stickleback feeding rate threshold (FRT).



light intensities above FRT but below MFRT. Alternatively, this result may be an artifact of an underestimation of FRT caused by the use of higher prey densities in the feeding experiments than exist in Kennedy Lake. These higher densities elevate encounter rates and, thus, may have stimulated feeding at lower light intensity than in the lake. Thus, we may underestimate the extent to which *S. oregonensis* avoid threshold light levels for stickleback feeding in the lakes.

An accurate estimate of MFRT was likely obtained from the laboratory experiments, because discrete time intervals occurred between prey encounters at the prey densities used. Above a certain prey density, one or more prey are always within view, and feeding rates are determined by light-independent pursuit, capture, and handling times. Below this prey density, time increments exist between encounters (i.e., the predator must search for its next prey). The encounter rates

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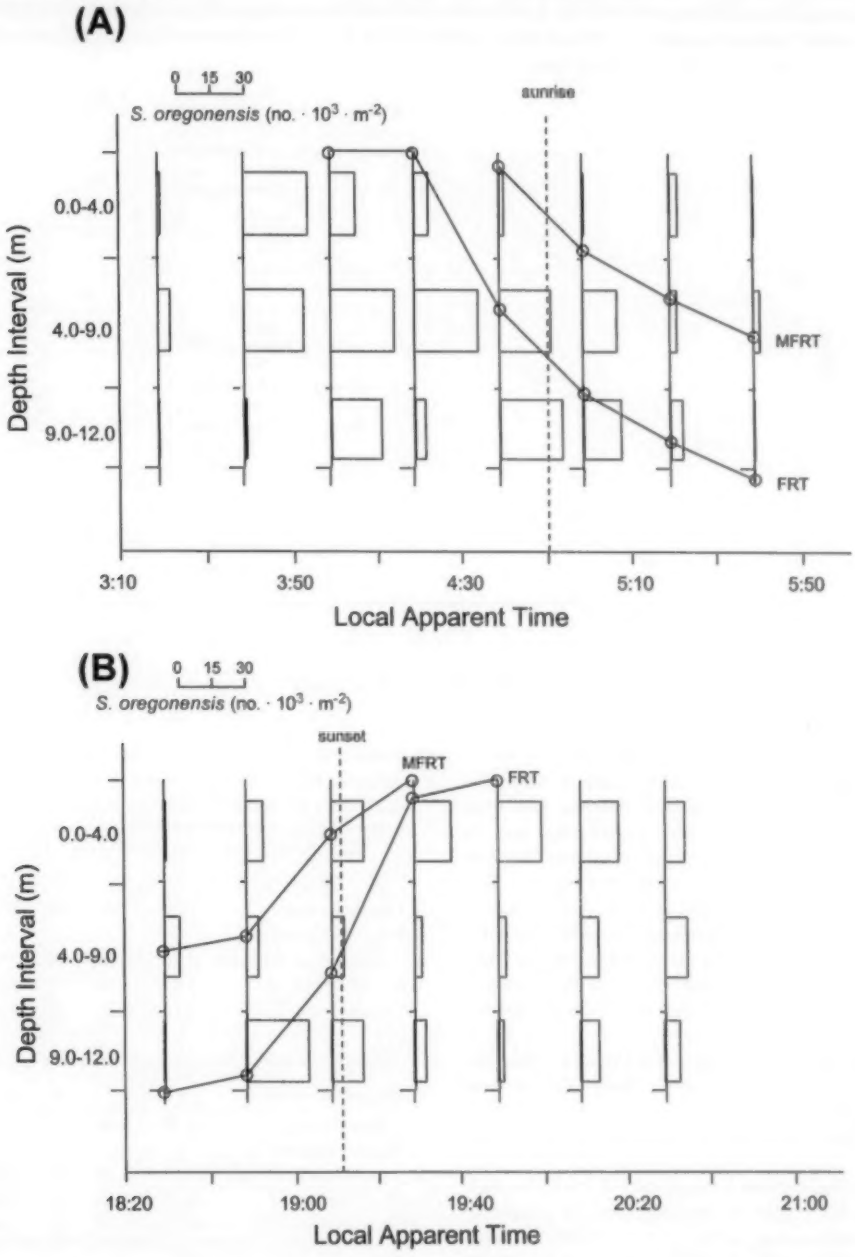
Fig. 5. Vertical migration of *S. oregonensis* relative to stickleback feeding rate thresholds in Paxton Lake during dawn (A) and dusk (B) on August 19, 1994. Details are as in Fig. 4.



are a function of reactive distances to prey, which are light dependent (Aksnes and Giske 1993; Ware 1973) but independent of prey density. Thus, maximum feeding rate will occur when further increases in light intensity have no further effect on reactive distances, and this will occur at the same light intensity for all prey densities below which time intervals occur between encounters.

Distinct time intervals between prey encounters were observed in the laboratory feeding experiments. This can be confirmed with simple time allocation calculations. With one exception, all fish in the experiment pursued less than 180 prey over a 15-min interval, and all prey encountered appeared to be pursued. We conservatively estimate a mean combined pursuit, capture, and handling time per prey item of 3 s. Even at 180 encounters, this leaves an average 2-s time interval between encounters.

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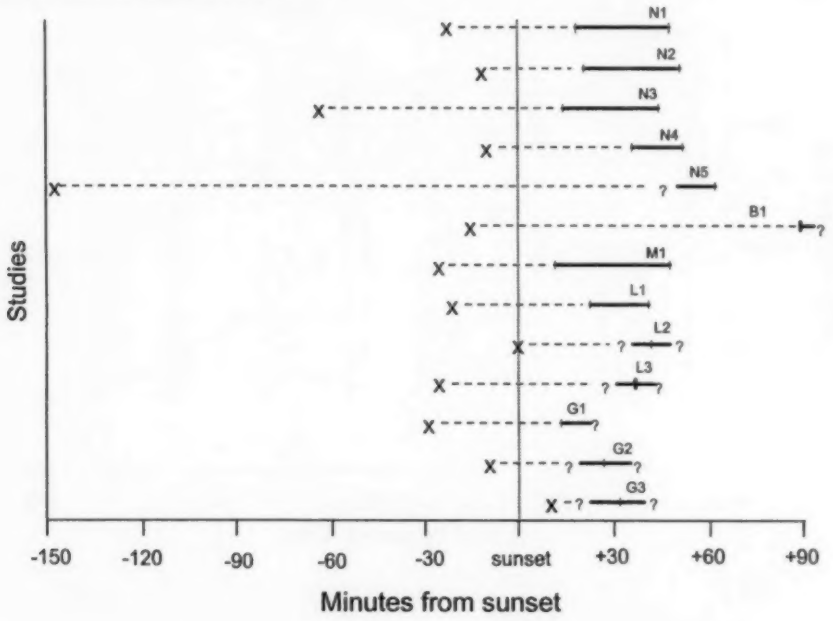
Fig. 6. Summary of available data on time of the beginning of movement of juvenile sockeye toward the surface (×), the period of migration toward the surface (broken lines) and the period of feeding near the surface (solid line) relative to sunset. Uncertainty about time that feeding begins or ends is represented by question marks. N1–N5 are from Narver (1970) at Babine Lake; B1 is from Barraclough and Robinson (1972) in Great Central Lake; M1 is from McDonald (1973) in Babine Lake; L1–L3 are from Levy (1989) in Shuswap Lake, Babine Lake, and Quesnel Lake; and G1–G3 are our data from Kennedy Lake.



Timing of *S. oregonensis* vertical migration relative to vertical migrations of juvenile sockeye and *N. mercedis*

Clearly, *S. oregonensis* did not decrease daytime risk from sockeye predation by migration; *S. oregonensis* were near the surface during the crepuscular feeding period of juvenile sockeye. In fact, descent to deep water during the day placed *S. oregonensis* closer to juvenile sockeye that also migrate downward and, thus, may have increased their risk. In Babine Lake, freshly eaten individuals of a vertically migrating copepod, *Heterocope septentrionalis*, were found in the stomachs of juvenile sockeye that occupied deep water during the day (Narver 1970).

Skistodiaptomus oregonensis did not decrease daytime risk from *N. mercedis* predation by migration. This predator moved to deep water during the day and only occupied near surface waters during dark periods when *S. oregonensis* were also near the surface.

The conclusion that vertical migration by *S. oregonensis* is neither driven by, nor results in, juvenile sockeye avoidance contradicts the conclusions of Schmidt et al. (1994) for copepods in turbid Alaskan Lakes. Possibly, the turbid conditions in these lakes force juvenile sockeye to feed in daylight near the surface, rather than crepuscularly and, thus, provide a daytime selective pressure for downward migration of zooplankton similar to that provided by stickleback in the lakes we studied. Hydroacoustic and trawl surveys indicate that juvenile sockeye remain near the surface throughout the diel period in turbid Owikeno Lake (Hyatt et al. 1989).

From hydroacoustic data, it has been inferred that juvenile sockeye in Nimpkish Lake undertake a nocturnal vertical migration rather than a typical diurnal migration and that daytime predation threat from these sockeye drove the observed zooplankton diurnal vertical migration in that lake (Levy 1990). However, pelagic stickleback are also present in Nimpkish Lake, and these may account for the zooplankton vertical migration. The sticklebacks may also account for the large number of surface fish targets in daytime hydroacoustic data that were interpreted as juvenile sockeye.

Table 2. Regression results for the effect of light (X) on four Y variables where $\ln(Y+1) = a\ln(X) + b$, except for the capture/strike ratio where $\arcsin((Y+0.01)^{0.5}) = a\ln(X) + b$.

(A) Light intensities ranging from 0.1 to 1.6 $\mu E \cdot s^{-1} \cdot m^{-2}$.

Dependent variable	a	b	n	r^2	F	$P>F$
Total prey eaten	1.06	3.54	42	0.37	23.98	0.0001
Skistodiaptomus oregonensis in guts	0.86	2.50	42	0.40	26.18	0.0001
No. of strikes	1.05	4.33	42	0.33	19.60	0.0001
Capture/strike ratio	0.12	0.77	36	0.20	8.48	0.02

(B) Light intensities ranging from 1.6 to 15.5 $\mu E \cdot s^{-1} \cdot m^{-2}$.

Dependent variable	a	b	n	r^2	F	$P>F$
Total prey in guts	0.34	3.44	24	0.11	2.64	0.1186
Skistodiaptomus oregonensis in guts	0.03	2.80	24	0.00	0.02	0.9033
No. of strikes	0.15	4.42	24	0.04	0.91	0.3510
Capture/strike ratio	0.083	0.078	24	0.20	1.51	0.50

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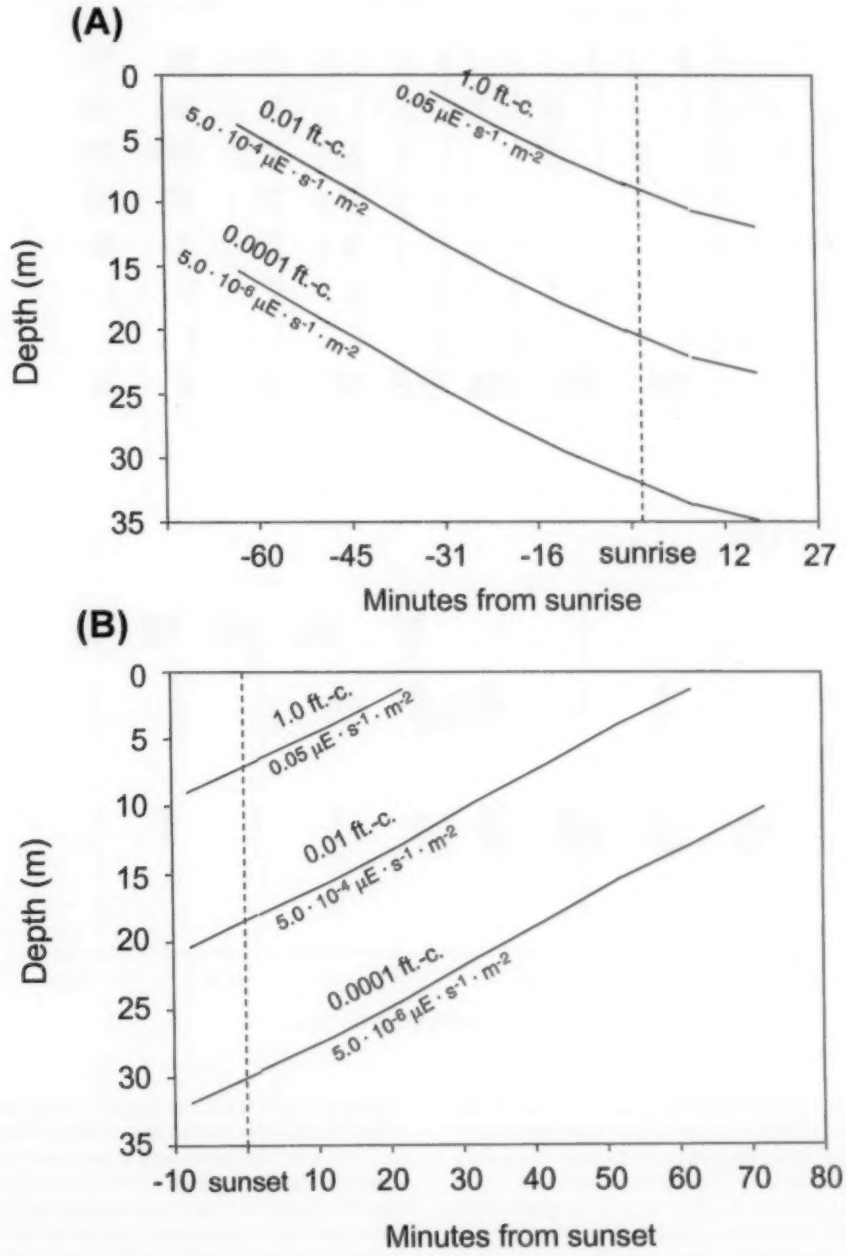
Fig. 7. Maximum (1.0 foot-candles; 1 foot-candle = 10.764 lx), half maximum (0.01 foot-candle), and minimum (0.0001 foot-candle) feeding rate depth isolumes for juvenile sockeye (Ali 1959) for clear sky conditions during dawn (A) and dusk (B) on June 23, 1994. Calculations were based on average clear sky instantaneous surface light intensities on June 23 at 50°N (U.S. Navy Bureau of Ships 1952) and an estimated light extinction coefficient of 0.401. Approximate quantum unit ($\mu E \cdot s^{-1} \cdot m^{-2}$) conversions for isolume values (using a wavelength of 555 nm) are also indicated.



Juvenile sockeye are visual feeders, and their crepuscular feeding strategy provides them sufficient light to feed efficiently while, presumably, still reducing the risk of predation by piscivorous fish (Ali 1959; Eggers 1978; Clarke and Levy 1988). Eggers (1978) suggested that this "control" of juvenile sockeye feeding strategy by piscivores may explain the lack of vertical migration by zooplankton in Lake Washington, Great Central Lake, and Babine Lake. Here we have confirmed that juvenile sockeye feeding in Kennedy Lake does not provide the type of selection pressure that drives the observed

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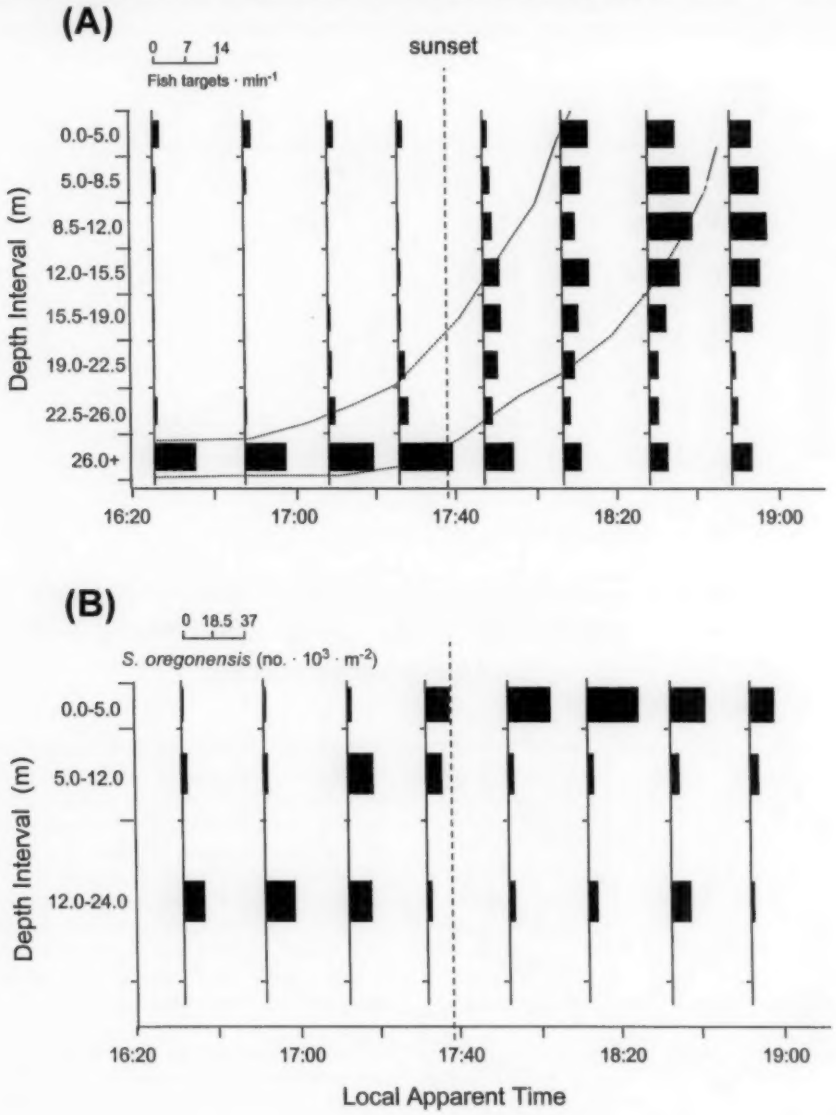
Fig. 8. Changes in vertical distribution of fish targets (A) and *S. oregonensis* (B) in Kennedy Lake at dusk on October 19, 1993. Upper and lower dotted lines are interpreted approximate timing of vertical movement of juvenile sockeye targets.



migration of *S. oregonensis* in Kennedy Lake. It remains to be understood why a vertical migration strategy does not evolve for *S. oregonensis* (or other copepod or cladoceran prey) such that they ascend later at dusk and earlier at dawn to avoid crepuscular juvenile sockeye feeding. A second question to address is what forces have selected for alternative feeding and predator avoidance strategies by diurnal feeding stickleback versus crepuscular feeding juvenile sockeye in Kennedy Lake?

***Skistodiaptomus oregonensis* vertical migration and separate juvenile sockeye and stickleback resource niches**

Stickleback and juvenile sockeye both utilize zooplankton resources that appear to be limited in many coastal lakes (O'Neill and Hyatt 1987; Hyatt and Stockner 1985) and are the only two common planktivores in many of these lakes (Hyatt and Stockner 1985). In lake enclosure experiments in Kennedy Lake the diets of both fish species were similar. Both preferred larger prey (including *S. oregonensis*) and strongly impacted the size distribution and species composition of the zooplankton community (O'Neill and Hyatt 1987). In the lake, however, juvenile sockeye are able to exploit vertically migrating *S. oregonensis*, but stickleback are not, because of the temporal segregation of their feeding activity. This may decrease the level of competition that may occur among these two planktivores in Kennedy Lake and some other coastal lakes (O'Neill and Hyatt 1987; Rogers 1968, 1973).

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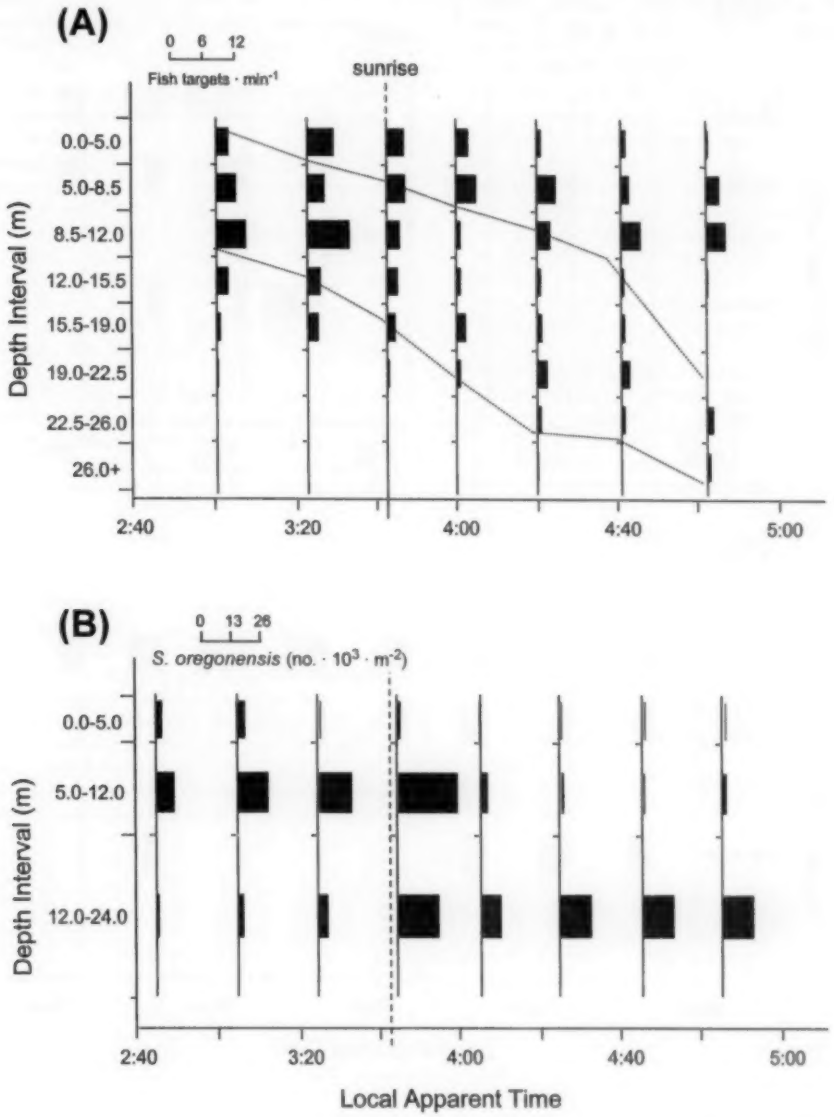
Fig. 9. Changes in vertical distribution of fish targets (A) and *S. oregonensis* (B) in Kennedy Lake at dawn on June 24, 1994. Other details are as in Fig. 8.



Skistodiaptomus oregonensis migration timing and the metabolic advantage hypothesis

Our results do not support the predictions of a model for a metabolic advantage hypothesis constructed by Enright (1977). That model predicts, under certain conditions, that vertically migrating zooplankton maximize growth by ascending toward the surface 1–2 h predusk to graze when phytoplankton density is maximal and remaining inactive in cold, deep waters for part of the diurnal period. The timing of *Calanus heterolandicus* migration fit this prediction during two spring sample periods, although during summer they migrated at dusk (Enright and Honegger 1977). In all our sample periods (May, June, August, and October), *S. oregonensis* in Kennedy Lake and Paxton Lake consistently migrated near sunset.

Summary

The extent and timing of *S. oregonensis* vertical migration in Kennedy and Paxton Lakes relative to the temporal spatial pattern of predation risk is consistent with the hypothesis that vertical migration by this species in these lakes is a stickleback avoidance adaptation. During daylight, *S. oregonensis* occupy depths at which light intensity reduces stickleback feeding rate. At dawn and dusk, migration is timed such that most *S. oregonensis* remain near or below the stickleback minumum

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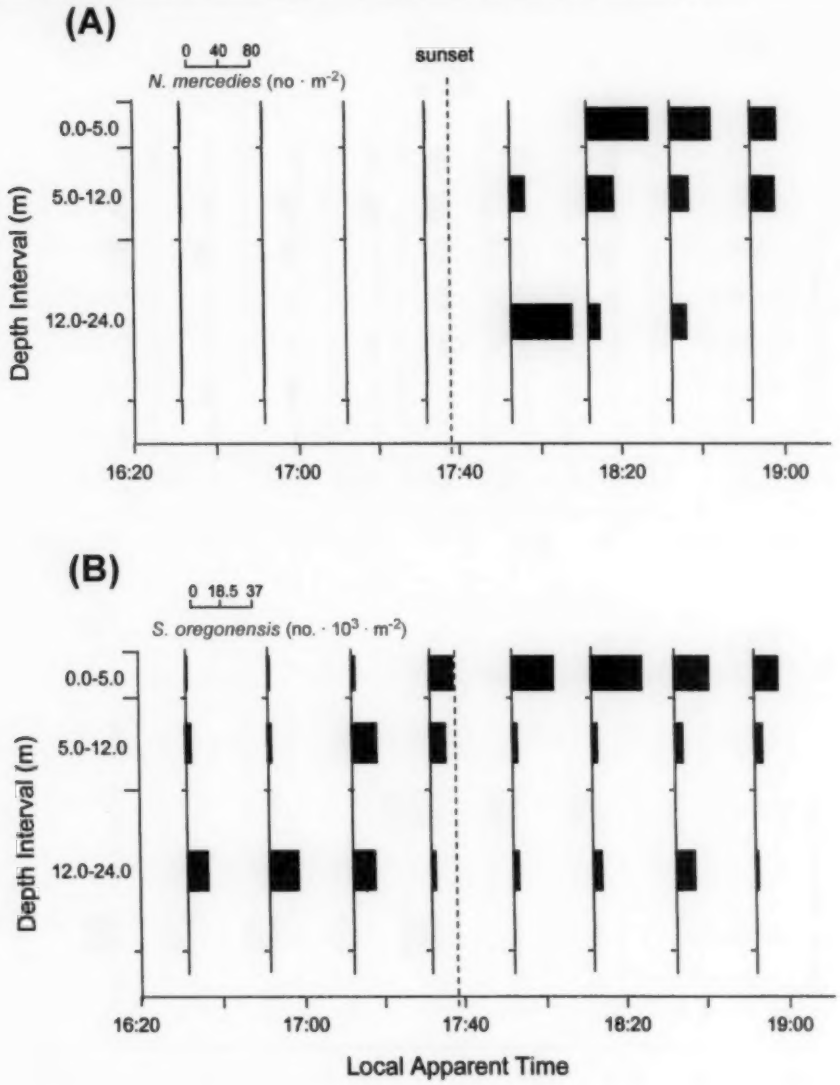
Fig. 10. Changes in vertical distribution of *N. mercedis* (A) and *S. oregonensis* (B) at dusk on October 20, 1993.



feeding rate threshold. In Kennedy Lake migration by *S. oregonensis* does not result in avoidance of predation from crepuscular feeding juvenile sockeye nor in avoidance of predation by the invertebrate *N. mercedis*.

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References

Aksnes, D.L., and Giske, J. 1993. A theoretical model of aquatic visual feeding. Ecol. Modell. **67**: 233–250.

Ali, M.A. 1959. The ocular structure, retinomotor and photobehavioral responses of juvenile Pacific salmon. Can. J. Zool. **37**: 965–996.

Angeli, N., Pinel-Alloul, B., Balvay, G., and Menard, I. 1995. Diel patterns of feeding and vertical migration in daphnids and diaptomids during the clear water phase in Lake Geneva (France). Hydrobiologia, **300/301**: 163–184.

Barraclough, W.E., and Robinson, D. 1972. The fertilization of Great Central Lake III. Effect on juvenile sockeye salmon. Fish. Bull. U.S. **70**: 37–48.

Bollens, S.M., and Frost, B.W. 1989. Predator-induced diel vertical migration in a planktonic copepod. J. Plankton Res. **11**: 1047–1065.

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Clarke, C.W., and Levy, D.A. 1988. Diel vertical migration by juvenile sockeye salmon and the antipredation window. Am. Nat. **131**: 271–290.

Eggers, D.M. 1978. Limnetic feeding behaviour of juvenile sockeye salmon in Lake Washington and predator avoidance. Limnol. Oceanogr. **23**: 1114–1125.

Enright, J.T. 1977. Diurnal vertical migration: adaptive significance and timing. Part 1. Selective advantage: a metabolic model. Limnol. Oceanogr. **22**: 856–872.

Enright, J.T., and Honegger, H.-W. 1977. Diurnal vertical migration: adaptive significance and timing. Part 2. Test of the model: details of timing. Limnol. Oceanogr. **22**: 873–886.

Ghan, D., Hyatt, K.D., and McPhail, J.D. 1998. Testing hypotheses for benefits and costs of vertical migration by *Skistodiaptomus oregonensis*: a population comparison approach. Can. J. Fish. Aquat Sci. **55**. This issue.

Hyatt, K.D., Rankin, D.P., and Rome, D. 1989. Acoustic census of limnetic fish in a glacially turbid lake. Proc. I.O.A. **11**(3): 238–247.

Hyatt, K.D., Rutherford, D., Gjernes, T., Rankin, P., and Cone, T. 1984. Lake enrichment program: juvenile sockeye unit survey guidelines. Department of Fisheries and Oceans, Nanaimo, B.C.

Hyatt, K.D., and Stockner, J.G. 1985. Responses of sockeye salmon (*Oncorhychus nerka*) to fertilization of British Columbia coastal lakes. Can. J. Fish. Aquat. Sci. **42**: 320–331.

Levy, D.A. 1989. The selective advantage of diel vertical migration behavior in juvenile sockeye salmon and kokanee (*Oncorhynchus nerka*). Ph.D. thesis, University of British Columbia, Vancouver.

Levy, D.A. 1990. Reciprocal diel vertical migration behaviour in planktivores and zooplankton in British Columbia lakes. Can. J. Fish. Aquat. Sci. **47**: 1755–1764.

Mangel, M., and Clarke, C.W. 1988. Dynamic modelling in behavioural ecology. Princeton University Press, Princeton, N.J.

McDonald, J. 1973. Diel vertical movements and feeding habits of underyearling sockeye salmon (*Oncorhynchus nerka*), at Babine Lake, B.C. Tech. Rep. Fish. Res. Board Can. No. 378.

McPhail, J.D. 1993. Ecology and evolution of sympatric sticklebacks (*Gasterosteus*): origin of species pairs. Can. J. Zool. **71**: 515–523.

Narver, D.W. 1970. Diel vertical migration and feeding of underyearling sockeye salmon and the limnetic zooplankton in Babine Lake, British Columbia. J. Fish. Res. Board Can. **27**: 281–316.

O'Neill, S.M., and Hyatt, K.D. 1987. An experimental study of competition for food between sockeye salmon (*Oncorhynchus nerka*) and threespine sticklebacks (*Gasterosteus aculeatus*) in a British Columbia coastal lake. *In* Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. *Edited by* H.D. Smith, L. Margolis, and C.C. Wood, Can. Spec. Publ. Fish. Aquat. Sci. No. 96. pp. 143–160.

Rogers, D.E. 1968. A comparison of the food of sockeye salmon fry and threespine sticklebacks in the Wood River lakes. *In* Further studies of Alaska sockeye salmon. *Edited by* R.L. Burgner. Univ. Wash. Publ. Fish. New Ser. **3**: 3–43.

Rogers, D.E. 1973. Abundance and size of juvenile sockeye salmon, *Oncorhynchus nerka*, and associated species in Lake Aleknagik, Alaska, in relation to their environment. Fish. Bull. U.S. **71**: 1061–1075.

Schmidt, D.C., Koenings, J.P., and Kyle, G.B. 1994. Predator-induced changes in copepod vertical migration: explanations for decreased overwinter survival of sockeye salmon. *In* Belle W. Baruch Libr. Mar. Sci. Vol. 18. Theory and application in fish feeding ecology. *Edited by* D.J. Stouder, K.L. Fresh, and R.J. Feller. University of South Carolina Press, Columbia, S.C. pp. 187–209.

U.S. Navy Bureau of Ships. 1952. Natural illumination charts. Res. Dev. Project No. NS 714-100. U.S. Navy Bureau of Ships, Washington, D.C.

Vanderploeg, H.A., and Scavia, D. 1979. Two electivity indices for feeding with special reference to zooplankton grazing. J. Fish. Res. Board Can. **36**: 362–365.

Ware, D.M. 1973. Risk of epibenthic prey to predation by rainbow trout. J. Fish. Res. Board Can. **30**: 787–797.

Zaret, T.M., and Suffern, J.S. 1976. Vertical migration in zooplankton as a predator avoidance mechanism. Limnol. Oceanogr. **21**: 804–813.

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Predicting the effects of rainbow smelt on native fishes in small lakes: evidence from long-term research on two lakes

Thomas R. Hrabik, John J. Magnuson, and Ann S. McLain

Abstract: We assessed predictability of negative interactions between native fishes and exotic rainbow smelt (*Osmerus mordax*) through field experiments and long-term data analysis for two lakes in Wisconsin. Predictions were made based on thermal preferences, diet characteristics, and published accounts of interactions between smelt and yellow perch (*Perca flavescens*) and smelt and cisco (*Coregonus artedii*). Our results indicate predation is the most likely cause for the extirpation of cisco from Sparkling Lake in 1990. In Crystal Lake, native yellow perch experienced significant overlap in distribution and diet with smelt. The condition of adult perch was negatively correlated with smelt abundance indicating competition was occurring. Smelt feed on a wide size range of prey items making this species a threat to native fishes, especially when spatial overlap is high. Information on spatial and temporal overlap and diet enable useful predictions about the effect of smelt invasions on native fishes.

Résumé : Nous avons étudié la prévisibilité des interactions négatives entre des poissons indigènes et l'éperlan arc-en-ciel (*Osmerus mordax*) exotique en réalisant des expériences sur le terrain et des analyses des données à long terme relatives à deux lacs du Wisconsin. Les prévisions ont été réalisées à partir des préférences thermiques, des caractéristiques des régimes alimentaires et des données publiées sur les interactions entre l'éperlan et la perchaude (*Perca flavescens*) et entre l'éperlan et le corégone (*Coregonus artedii*). Nos résultats montrent que la prédation est la cause la plus probable de la disparition du corégone dans le lac Sparkling en 1990. Dans le lac Crystal, il y avait un chevauchement significatif de la répartition et du régime alimentaire de la perchaude indigène et de l'éperlan. L'état des perchaudes adultes était corrélé négativement avec l'abondance de l'éperlan, ce qui indique qu'il y avait compétition entre les deux espèces. L'éperlan se nourrit de proies de tailles très diverses et représente donc une menace pour les poissons indigènes dont le domaine vital chevauche celui de l'éperlan. Les données sur le chevauchement spatial et temporel et sur le régime alimentaire permettent de faire des prévisions utiles concernant l'effet des invasions d'éperlans sur les poissons indigènes.
[Traduit par la Rédaction]

Introduction

Exotic fishes have lead to changes in native fish community structure in many aquatic ecosystems (Moyle 1986; Kaufman 1992; Lodge 1993). In recent years, many North American lakes have been invaded by exotic and native fishes that have expanded their range (Crossman 1991). Species invasions have played an especially important role in restructuring fish communities in the Laurentian Great Lakes (Wells and McLain 1972; Crowder 1980, 1986; Kitchell and Crowder 1986) as well as smaller inland lakes (Colby et al.1987; Crossman 1991). A particular Great Lakes exotic, the rainbow smelt (*Osmerus mordax*), has been introduced or has invaded many smaller lakes in the upper Great Lakes region in Canada (Franzin et al. 1994) and the United States, and native fish species have suffered as a result (Evans and Loftus 1987; Colby et al.1987; Evans and Waring 1987).

While the spread of smelt and other exotic fishes will inevitably continue, predicting effects of exotic fishes on native fish communities is important to managing fisheries in affected water bodies and to preserving the integrity and stability of native species assemblages. Introductions of smelt have not been detrimental to native fish communities in all cases, but many examples show significant negative effects. Most recent studies citing the negative effects of rainbow smelt indicate predation as the most important mechanism. Smelt predation has been linked to reduced recruitment and the decline of native fishes, particularly coregonids (e.g., Crowder 1980; Loftus and Hulsman 1986; Evans and Loftus 1987). In all instances, spatial overlap between adult smelt and native fish larvae and the resulting predation ultimately led to declines in recruitment and population density. Negative impacts by smelt via competition also have been addressed (Anderson and Smith 1971; Crowder 1980, 1986), but the effects of competition resulting from the establishment of rainbow smelt and its importance in different environments, has not been adequately tested in the field (Evans and Loftus 1987).

Our intent here was to assess predictability of the effects of rainbow smelt on native fishes and to determine which predictors are most useful. We addressed interactions between invading smelt and the historically dominant, native cisco (*Coregonus artedii*) and yellow perch (*Perca flavescens*) in each of two lakes as smelt increased. We hypothesized that interactions will be governed by spatial overlap, similarity in

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feeding, and predation, with spatial overlap being an important component to interaction intensity.

We used long-term data supplemented with additional field studies describing the diet, growth, and distribution of the fish species to determine whether smelt had negative effects on native species in each of the lakes and by what mechanisms.

Materials and methods

Study sites

Crystal and Sparkling lakes are small oligotrophic lakes located in Vilas County, Wisconsin, that are studied by the North Temperate Lakes – Long-term Ecological Research project (NTL–LTER) (see Magnuson et al. 1984, 1994). Sparkling Lake is a 68-ha seepage lake with a maximum depth of 20 m and approximately 50% of its area deeper than 7 m in depth. Secchi depth during the ice-free season averages approximately 6 m. Its littoral zone is narrow, with emergent and submergent vegetation, abundant coarse woody debris, and rocky boulder habitat. Portions of the hypolimnion become anoxic in late summer, but fish kills as a result of anoxia have never been noted, and significant portions of the hypolimnion remained oxygenated during the entire study period. Crystal is a 46-ha precipitation-dominated lake with a maximum depth of 20.5 m and over 50% of its area greater than 7 m. The Secchi depth during the ice-free season averages approximately 9 m. The hypolimnion of Crystal Lake rarely exhibits anoxic conditions. The littoral zone is sandy, with little course woody debris and few macrophytes. Crystal Lake contains few piscivorous fish and supports no substantial recreational fishery.

Long-term data collection

The NTL–LTER conducts a yearly fish survey during which relative abundance, length, and mass data are collected on fish communities using six different sampling gears (see Magnuson et al. 1994). We used yearly NTL–LTER survey data from 1981 to 1994 to obtain estimates of relative abundance, age structure, as well as measures of relative condition for fish present in Crystal and Sparkling lakes.

Trends in relative condition of smelt and perch in Crystal Lake and smelt and cisco in Sparkling Lake were assessed using a linear weight versus total length relationship for each species. The linear model was applied to log-transformed body mass and total length data pooled according to species and lake from NTL–LTER fish surveys that took place from 1981 to 1994. Fish <75 mm were excluded from the analysis because of error associated with measuring their mass in the field. The mean residual for each species in each year represented the relative condition of fish >75 mm of each species in each respective year.

Field studies

Diet, distribution, growth, and (or) relative condition of each native fish species and smelt were monitored in each lake. Fish were collected using vertical gillnets ranging from 19- to 89-mm bar mesh set in the deep basin of each lake. The overlap in vertical distribution of Crystal Lake perch and smelt and Sparkling Lake cisco and smelt across a thermal strata was determined by applying Schoener's (1970) proportional overlap to distribution data for both species collected by the LTER program during August of 1981–1993. Thermal overlap was calculated using the epilimnion, metalimnion, and hypolimnion as resource strata. We considered the epilimnion the area above the depth at which the temperature decreased 1°C or more within a metre, the metalimnion included the area where temperature decreased more than $0.99°C \cdot m^{-1}$, and the hypolimnion was considered the area below the metalimnion. Thermal overlap in Crystal Lake during the thermally stratified period of 1994 was also estimated to asses seasonal patterns of overlap in a year of high smelt abundance.

In Sparkling Lake, fish diet samples were collected from fish caught in gillnets set for 1–5 h. The digestive tract of each fish was removed and individually preserved in 10% buffered formalin and later examined. In Crystal Lake, diet samples were collected using shorter duration gillnet sets (30–90 min), and the fish were immediately placed on ice to curtail digestion. Diet selectivity was estimated for perch and smelt in Crystal Lake only. Prey abundance and distributions were estimated using a 2-m long, 45-L Schindler–Patalas trap. Feeding preferences of perch and smelt were determined using Chesson's alpha (see Chesson 1978) and presented graphically using Vanderploeg and Scavia's (1979) relativized E^*. Diet overlap between smelt and perch in Crystal Lake was assessed using Hurlbert's (1978) index of niche overlap on diet and zooplankton data collected during 1992 and 1994.

Stomachs of fish collected in 1994 were weighed before being emptied so that the mass of food in them could be estimated. The mass of the empty stomach was calculated based on a linear relationship between empty stomach mass and body mass for both perch and smelt. These relationships were obtained by weighing the stomachs of fish starved for 48 h in the laboratory and calculating linear relationships between stomach mass and fish mass. For smelt, empty stomach mass was equal to 0.017(fish mass) + 0.034 ($r^2 = 0.966$). For perch, empty stomach mass was equal to 0.012(fish mass) + 0.010 ($r^2 = 0.953$). The generalized gastric evacuation model presented in He and Wursbaugh (1993) was then applied using the estimated food masses and temperature data obtained from field samples. This allowed correction for food left over from feeding bouts prior to the sampling period in which each fish was collected.

Age and growth of fishes were determined using scale analysis. For cisco, scales were collected during yearly LTER surveys from 1981 to 1989. Fish lengths at each scale annulus were back calculated using the linear regression method described by Bagenal and Tesch (1978), and 55 mm as the size at which cisco become completely scaled (Hogman 1970). For perch, a von Bertalanffy growth curve (Ricker 1958) was calculated using scale data to allow ages to be estimated for each fish caught in each year throughout the long-term record.

Results

Changes in native fish communities

Historically, cisco dominated the pelagic fish community in Sparkling Lake (Hile 1936). Smelt replaced cisco as the dominant fish species by 1985 (Fig. 1). Cisco declined to low abundance during 1987, 1988, and 1989 and were not detected in yearly LTER fish surveys after 1990. The age distribution of cisco shows that most fish caught after 1982 were born in 1981 and 1982 (Table 1). After the smelt invasion, the absence of young-of-the-year (YOY) and 1+ fish gillnet catches between 1985 and 1990 reveals the dramatic decline in young cisco survival (Table 1). Larval cisco were present during the spring of 1987, moderately abundant in May 1988, and present in June 1988, indicating that adult cisco were producing offspring during the population decline (McLain 1991). The young cisco were not, however, surviving their first year of life.

The fish community in Crystal Lake was historically dominated by yellow perch. Smelt were detected by the yearly NTL–LTER fish survey in 1985 and reached high abundances in 1993 and 1994 replacing perch as the dominant fish species (Fig. 1). Perch were abundant during the 1980s and early 1990s, suggesting that any interaction occurring between the two species did not have an immediate effect on the density of perch. In contrast to Sparkling Lake cisco, Crystal Lake perch did have successful reproduction and recruitment after adult smelt were numerous (Table 1). Perch abundance, however,

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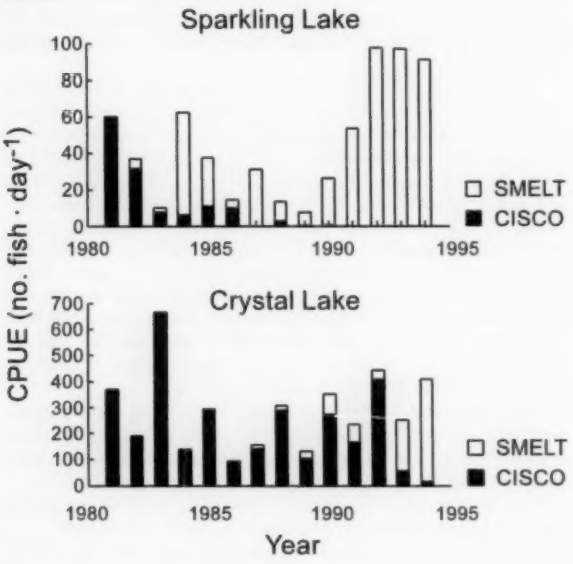
Fig. 1. Gillnet catch per unit effort (CPUE) standardized for a 24-h set for smelt and cisco in Sparkling Lake. CPUE was summed over all gears for perch and smelt in Crystal Lake from 1981 to 1994. Abundance for Crystal Lake was presented as total CPUE because of smelt and perch being frequently caught in more than one gear. In Sparkling Lake, smelt and cisco are caught predominantly in gillnets.



has recently declined with 1994 showing the lowest abundance level recorded (Fig. 1).

Diet characteristics

Diet samples from 1985 to 1989 show that adult smelt and cisco in Sparkling Lake ate zooplankton, aquatic stages of insects, and small fish (Table 2). While zooplankton were the most prevalent diet item in adult smelt and cisco stomachs, each species consumed small fish and a relatively high proportion of the smelt caught often contained small fish (Table 2).

In Crystal Lake, diets of smelt and perch most consistently contained zooplankton. In 1992, both species also ate fish and insect larvae, and a fairly high proportion of smelt contained fish in their diet relative to perch. In 1994, however, zooplankton and insect larvae and pupae were the most prevalent diet items found.

In Crystal Lake, we conducted detailed field sampling on fish diet characteristics, feeding selectivity, and feeding chronology. The feeding rate of perch and smelt was highest during the day for both species in 1994 (Fig. 2). The maximum smelt feeding rates in Crystal as well as Sparkling Lake occurred during midmorning (Fig. 2). Crystal Lake smelt also fed in the evening, with feeding decreasing thereafter until reaching the lowest level just before dawn (Fig. 2). Perch feeding in Crystal Lake was maximum during the early afternoon with secondary periods of feeding activity at dawn and dusk. Feeding rates were lowest during the midafternoon and predawn periods (Fig. 2).

Diet selectivity of Crystal Lake smelt and perch collected in 1994 indicates that both species select small and large

Table 1. Age frequency of Sparkling Lake cisco and Crystal Lake perch caught in August in each year.

(A) Sparkling Lake cisco

	Year									
Age	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990
0+	79	2								
1+	31	53	1	2						
>1+	7	3	14	10	22	20		6	1	1

(B) Crystal Lake perch

	Year									
Age	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994
0+		24	68	93			25	4	66	
1+	74	3	47	666	132	7		3	19	1
>1+	523	177	251	56	118	574	363	820	129	47

crustacean zooplankton, during the day (Fig. 3). At night, perch selected small zooplankton, but *Daphnia* were largely not eaten during low light. The high electivity for bosminids as well as cyclopoid copepods may be an artifact of low consumption of prey resources by perch at night, with both prey items making up a large proportion of the diet of perch relative to that found in the environment. The absence of *Daphnia* in perch diets at night suggests that a decrease in the effectiveness of perch visual feeding at low light levels reduced the amount of larger zooplankton consumed by this species. Smelt exhibited high preference for *Daphnia* under the same low light conditions and appear at least somewhat capable of feeding selectively at night (Fig. 3). The small amounts of food eaten by both species at night relative to that consumed during the day, however, suggests that food resources present during the day are the most important for both species (Figs. 2 and 3).

Prey preferences for both fish species in 1992 were strikingly different from those in 1994, but each species preferred similar prey to each other in each year. Perch and smelt both preferred *Daphnia* over all other zooplankton in 1992 with *Daphnia* and cyclopiod copepods being the most numerically common zooplankton prey (Fig. 3). In 1994, perch and smelt preferred cyclopoid copepods, *Daphnia* and bosminids, which were the most common zooplankton found in their diets. Bosminids and cyclopoids were eaten by both perch and smelt in 1992 but were preferred less than in 1994. Differences in prey selectivity between perch and smelt on *Leptodora* in 1994 and bosminids in 1992 were apparent but of little consequence, as each of the two prey items made up less than 2% of the diet on any sampling date in each year.

Overlap in prey resource use (L) (see Hurlbert 1978) by perch and smelt in 1992 ranged from less than one in early June to >600 times more likely than if the two species had fed at random in late June (Fig. 4*a*). In 1994, diet overlap was approximately eight times greater than expected had both species selected prey at random during late summer and early fall (Fig. 4*b*). Diet overlap was maximal during the peak of the growing season in 1994 when sampling extended from late May to November.

Length distributions of *Daphnia* and *Diacyclops*, the most common zooplankton in the diets of both species in 1994 were significantly different than the length distributions of both *Daphnia* and *Diacyclops* observed in the environment

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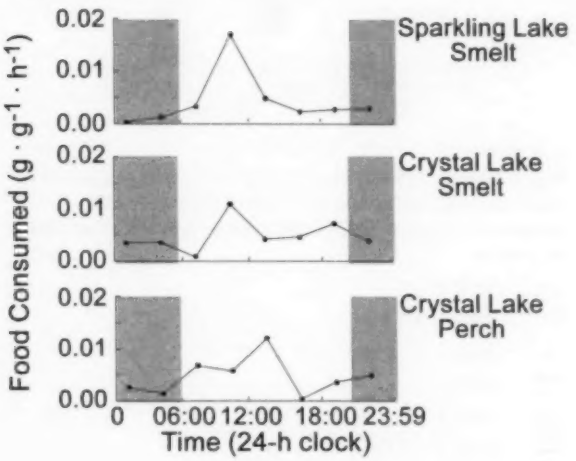
Table 2. Diet composition of cisco and smelt in Sparkling Lake and perch and smelt in Crystal Lake.

Lake	Species	Date	Zooplankton	Insects	Fish	*N*
Sparkling	Cisco	May–June 1986	0.72	0.17	0.06	18
	Smelt	August 1985	0.21	0.53	0.26	19
		May–June 1986	0.15	0.74	0.08	39
		August 1988	0.56	0.67	0.44	9
Crystal	Perch	May–July 1992	0.88	0.30	0.04	87
	Smelt	May–July 1992	0.76	0.37	0.42	38
	Perch	May–July 1994	0.61	0.38	<0.01	89
	Smelt	May–July 1994	0.72	0.34	<0.01	135

Note: Values are the proportion of the total fish collected that contained each diet item.

Fig. 2. The average mass of food in smelt and perch stomachs corrected for stomach evacuation rates estimated for fish collected over the 24-h cycle in Crystal Lake and Sparkling Lake in 1994. Shaded areas indicate low light levels. Equations taken from He and Wurtsbaugh (1993) were used to correct for stomach evacuation rates.



(Kolomogorov–Smirnov paired distribution test; $a < 0.05$) (Fig. 5). The length distributions of *Diacyclops* and *Daphnia* found in the stomachs of smelt and perch did not statistically differ (Kolomogorov–Smirnov paired distribution test, $a > 0.50$), indicating that perch and smelt selected similar sized individuals of each prey type (Fig. 5).

Thermal distribution

We caught YOY cisco in the epilimnion of Sparkling Lake during May and early June of 1988, but our sampling of adult fish during May from 1986 through 1988 yielded no adult smelt <4 m in depth (McLain 1991). Over 80% of our smelt catch occurred in depths of 10 m or greater (McLain 1991). In 1981, a year when substantial number of young of year and adult cisco were caught in vertical gillnets during the NTL–LTER fish sampling, YOY cisco were located in the cold-water areas along with the adult (median temperature for YOY cisco 7.9 ± 1.9°C; mean ± SD) moved from the epilimnion to hypolimnetic areas of Sparkling Lake between early June and August. Thermal resource use by smelt and cisco in Sparkling Lake indicated thermal overlap between smelt and cisco averaged approximately 55% over the 8 years the two species co-occurred and was over 50% during August in every year but 1982 (Fig. 6*a*).

Thermal resource overlap by smelt and perch in Crystal Lake ranged from 30 to 70% during August from 1986 to 1993 (Fig. 6*b*). The years of 1990 and 1993 had the highest overlap (Fig. 6*b*), with values over 60%. The overlap between perch and smelt also increased in relation to the historical average after 1989 and remained near 50% after 1990. The seasonal overlap during 1994, a year with extremely high adult smelt abundance, showed greater than 60% overlap in May, July, and August (Fig. 6*c*) suggesting that increases in smelt abundance may have led to increases spatial overlap.

Relative condition of perch in Crystal Lake declined significantly and progressively as smelt increased in abundance ($r = 0.741$, $p < 0.05$ for perch relative condition vs. the natural log of smelt catch per unit effort). The relative condition of perch and smelt was correlated ($r = 0.824$, $p < 0.05$) indicating that both species responded similarly to environmental changes that occurred in the lake throughout the record. These results indicate that the average individual of both species realized a decrease in feeding success with the increase in smelt abundance and responded similarly to changes in their environment (Fig. 7).

In Sparkling Lake, increases in smelt abundance had no negative effect on the relative condition of cisco or smelt (Fig. 7). In 1986, cisco relative condition was significantly below the historical mean. With this exception, cisco condition in years prior to, as well as after, 1986 was either not significantly different or was higher than the historical average (Fig. 7). The results of scale analysis on cisco hatched before and after the smelt invasion indicates that the average length of cisco at the first annulus was not significantly different before and after the smelt invasion (*t* test, $t = 1.125$, $p = 0.225$, $df = 118$). The relative condition of Sparkling Lake smelt was variable and showed no significant pattern (Fig. 7).

Discussion

Predicting the effects of smelt on native fishes in regions where smelt are spreading is of interest to ecologists, lake managers, and the public. Smelt often negatively influence native fishes when introduced in freshwater lakes. Evans and Loftus (1987) provided 26 case studies where smelt were introduced into lakes with non-coevolved species; 18 cases had negative impacts on a native species. Prediction of negative impacts may be possible if information is available on native species in lakes likely to be invaded. Prior information on native fish

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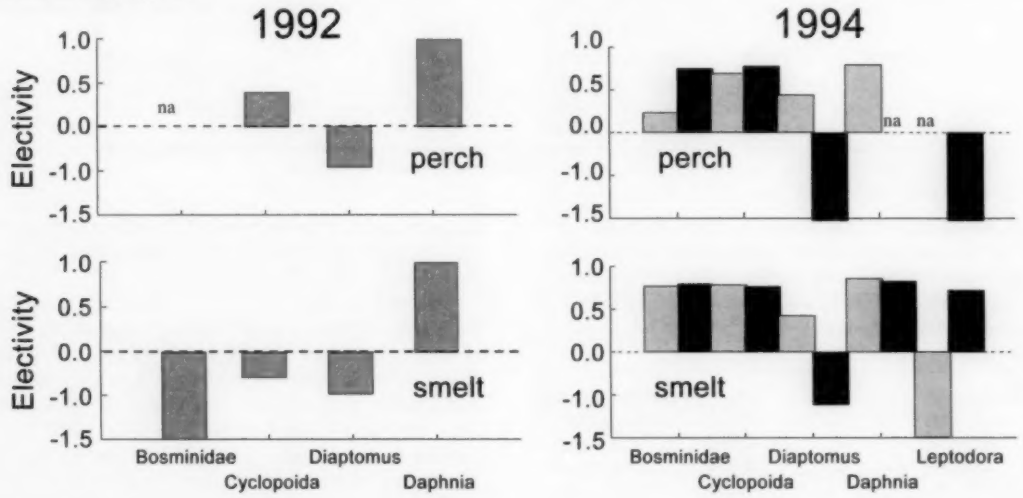
Fig. 3. Prey electivities for the most common zooplankton prey in perch and smelt stomachs from Crystal Lake in 1992 and 1994. Electivities for 1994 were calculated for day and night across 2-m depth intervals for both fish and prey. Solid bars represent estimates for fish and zooplankton collected at night; shaded bars represent estimates for fish and zooplankton collected during the day. Electivities for 1992 were calculated from fish collected during the day, dusk, and night and zooplankton abundance from day samples. Values represent weighted means using fish from all sampling dates.



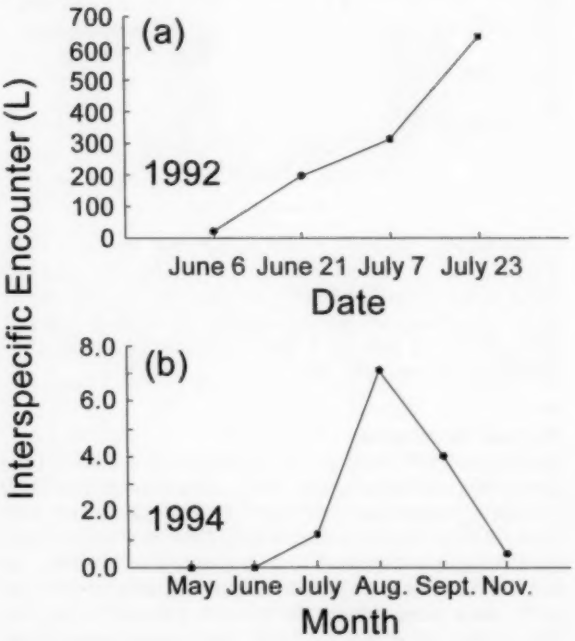
species in the lakes or watersheds of concern, however, are often absent or limited. Obtaining data on the characteristics of fish populations is costly and labor intensive. Thus, prediction of smelt effects based on specific, attainable parameters would be beneficial to assessing potential lake management strategies.

In both Crystal Lake and Sparkling Lake, smelt and native species used similar thermally defined areas. In Sparkling Lake, smelt and cisco preferred cold-water areas and exhibited substantial overlap in thermal distribution (Fig. 6). Overlapping distributions of cisco and smelt did not reduce feeding success of cisco, but predation on young cisco forced to occupy cold water by life-history traits has apparently lead to recruitment failure. Thermal overlap in this case may have placed young cisco in close proximity to predatory adult smelt during the summer months and indirectly led to the extirpation of cisco from the lake by 1990; only 8 years after smelt were detected.

In contrast, thermal overlap between perch and smelt in Crystal Lake resulted in reduced feeding success for perch because of similarity in prey resource use relative to smelt. Increases in smelt abundance led to a progressive decline in the relative condition of perch showing the negative effects of competition with smelt. Unlike young cisco, however, juvenile perch in Crystal Lake are distributed in shallow areas of the epilimion and in the littoral zone (T. Hrabik, unpublished data). Furthermore, recruitment of Crystal Lake perch is known to have occurred in recent years. McCauley and Read (1973) showed that juvenile perch preferred temperatures warmer than adult perch, with a final preferendum near 23°C. Thus, juvenile perch may avoid extended periods of predation from adult smelt because of a much warmer thermal preference.

Without question, the most accurate assessment of interaction intensity will come from actual measurements of smelt

Fig. 4. Hurlbert's (1978) measure of diet overlap (L) calculated for perch and smelt in Crystal Lake biweekly for the early to midsummer period of 1992 (*a*) and monthly for the ice-free season of 1994 (*b*).



and native fish resource use in each system invaded by smelt. However, managers are often faced with implementing management strategies based on little or no information. There are very few studies that document thermal occupancy of smelt in

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Fig. 5. Length–frequency distributions of *Diacyclops* and *Daphnia* in the environment and those found in smelt and perch stomachs in Crystal Lake in 1994. Distributions with an asterisk are significantly different from the length distribution found in the environment. Differences in distributions were tested using a Kolmogorav–Smirnov paired distribution test with $\alpha = 0.05$.

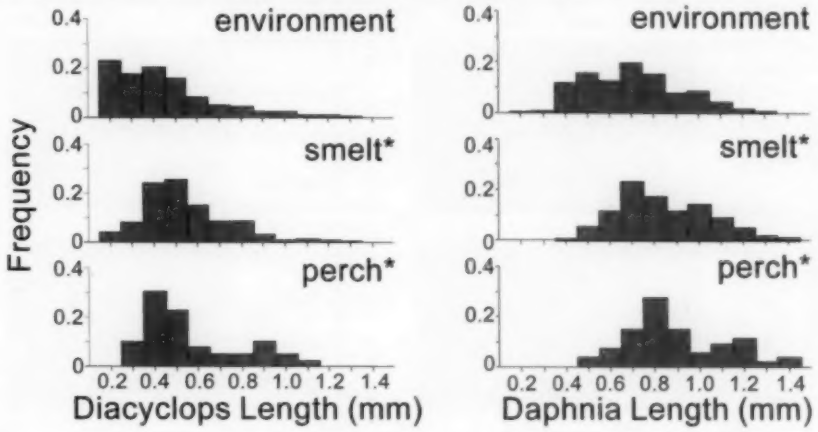
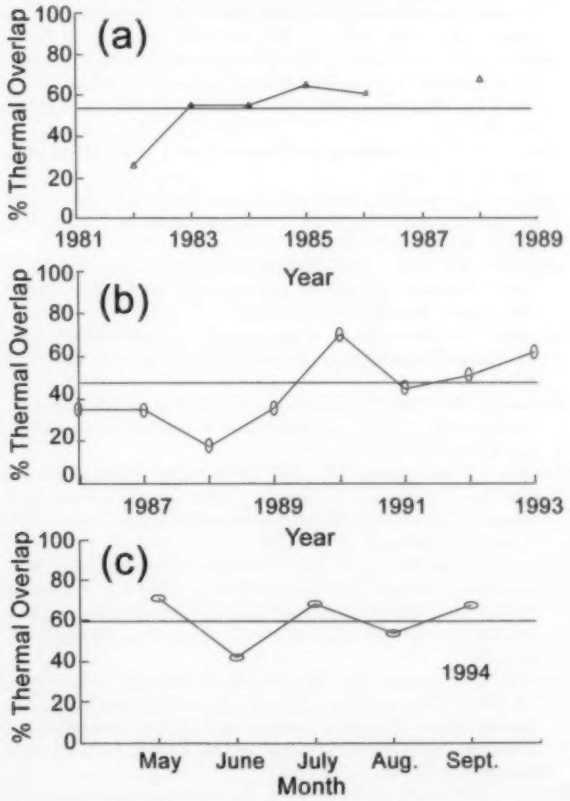


Fig. 6. Thermal niche overlap calculated using the epilimnion, metalimnion, and hypolimnion thermal strata as resource states for historical data collected on Crystal Lake from 1985 through 1993 (*a*) and Sparkling Lake from 1982 through 1989 (*b*). Thermal niche overlap for perch and smelt in Crystal Lake in 1994 over the thermally stratified portion of the ice-free season (*c*). The horizontal line in all panels shows the historical mean.



small lakes. Our estimates of smelt thermal preference in both Crystal and Sparkling lake are similar to those found in other lakes (see Wismer and Christie 1987). Based upon our findings and published thermal preferendum (see Wismer and Christie 1987), smelt are found consistently between 8 and 16°C, with 12–13°C being the most common temperature preferrendum. Given the apparent consistency in smelt thermal preference, smelt thermal distribution could be estimated and compared with thermal distributions of native fish in waterbodies expected to be invaded by smelt prior to an invasion taking place. This type of prior assessment would allow management action to be taken previous to any potential negative effects taking place.

Published thermal preferences for adult perch, however, show that yellow perch exhibit variability in thermal preferendum, and preferences may be dependent upon the population and season with final preferendum ranging from 7 to 30°C and most commonly occurring between 19 and 22°C (Wismer and Christie 1987). During our study, thermal occupation by yellow perch in Crystal Lake during summer averaged approximately 16°C, which is below the temperature perch most commonly prefer. Thus, predicting interactions between species with wide thermal tolerances should not be considered without collecting information on specific populations of concern.

Predation effects by smelt include recruitment reductions, population declines, and potentially the extirpation of the native species. Spatial overlap between smelt and native fish, with a body diameter smaller than the gape of adult smelt, will likely result in predation effects by smelt on the native fish. Negative effects of predation would likely manifest in reductions in recruitment, native species population declines and possibly the extirpation of the native species.

Interspecific competition occurs when common limiting resources are utilized by more than one species with the extent of overlap in resource use potentially dictating the strength of competition (Larkin 1956). While overlap in spatial distribution indicates that competition is possible, competition may also occur if there is no overlap in distribution but other

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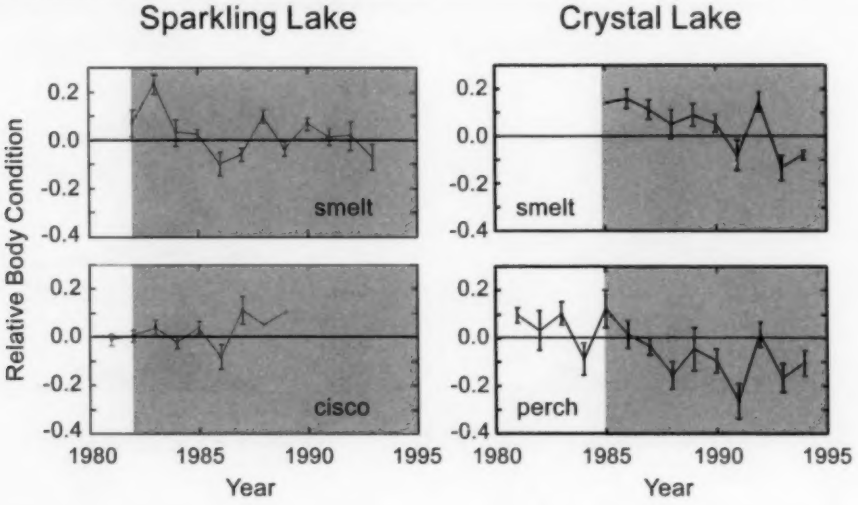
Fig. 7. Relative condition of smelt and cisco in Sparkling Lake and smelt and perch in Crystal Lake from 1981 to 1994. Shaded areas indicate dates after smelt were detected. Error bars are 95% confidence intervals.



resources are being shared. For example, if two fish species feed on zooplankton that perform diel vertical migration in the water column, each species may utilize the same food resource during different periods of the day. Thus, while no spatial overlap may occur between smelt and native species, utilization of the same food resource may cause a reduction in the success of the native species resulting from consumption by smelt. If two species overlap in distribution and have similar prey preferences, however, competition is more likely because of the high potential for common use of spatial as well as food resources. Detailed diet information is needed to accurately predict exploitation competition. Potential effects of competition would include a shift in resource use after an invasion, a reduction in the fitness of the native as a result of resource use, and reductions in the population level of the native species.

Our study shows that smelt had strong negative effects on native fishes both NTL–LTER study lakes that have been invaded. The mechanisms of interactions in each case were unique, but spatial overlap is common to each case. Plasticity in the habitat choices of fishes is common making comparisons between generalized thermal preferences, and diet characteristics of smelt and native species are uncertain predictors of species interactions at best. Prior information on native fish spatial distribution and prey resource use along with information on invading smelt is essential to accurately predicting competitive interactions and predation effects. Finally, any purposeful introduction of smelt into freshwater lakes should be done with great caution; the ability of smelt to effectively consume a wide range of prey makes introducing this species an uncertain proposition at best.

Acknowledgements

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References

Anderson, E.D., and Smith, L.L. 1971. Factors affecting abundance of lake herring (*Coregouns artedii* Lesueur) in western Lake Superior. Trans. Am. Fish. Soc. **100**: 691–707.

Bagenal, T.B., and Tesch, F.W. 1978. Age and growth. *In* Methods for assessment of fish production in fresh waters. 3rd ed. *Edited by* T.B. Bagenal. Blackwell Scientific Publishers, Oxford. pp. 131–136.

Chesson, J. 1978. Measuring preference in selective predation. Ecology, **59**: 211–215.

Colby, P.J., Ryan, P.A., Schupp, D.H., and Searns, S.L. 1987. Interactions in north-temperate lake fish communities. Can. J. Fish. Aquat. Sci. **44**(Suppl. 2): 104–128.

Crossman, E.J. 1991. Introduced freshwater fishes: a review of the North American perspective with emphasis on Canada. Can. J. Fish. Aquat. Sci. **48**(Suppl. 1): 46–57.

Crowder, L.B. 1980. Alewife, rainbow smelt and native fishes in Lake Michigan: competition or predation? Environ. Biol. Fishes, **5**: 225–233.

Crowder, L.B. 1986. Ecological and morphological shifts in Lake Michigan fishes: glimpses of the ghost of competition past. Environ. Biol. Fishes, **16**: 147–157.

Evans, D.O., and Loftus, D.H. 1987. Colonization of inland lakes in the Great Lakes region by rainbow smelt, *Osmerus mordax*: their freshwater niche and effects on indigenous fishes. Can. J. Fish. Aquat. Sci. **44**(Suppl. 2): 249–266.

Evans, D.O., and Waring, P. 1987. Changes in the multispecies, winter angling fishery of Lake Simcoe, Ontario, 1961–83: invasion by rainbow smelt (*Osmerus mordax*) and the roles of intra- and interspecific interactions. Can. J. Fish. Aquat. Sci. **44**(Suppl. 2): 182–197.

Franzin, W.G., Barton, B.A., Remnant, R.A., Wain, D.B., and Pagel, S.J. 1994. Range extension, present and potential distribution, and possible effects of rainbow smelt in Hudson Bay drainage waters of northwestern Ontario, Manitoba and Minnesota. N. Am. J. Fish. Manage. **14**: 65–76.

He, E., and Wurtsbaugh, W.A. 1993. An empirical model of gastric

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evacuation rates for fish and an analysis of digestion in piscivorous brown trout. Trans. Am. Fish. Soc. **122**: 717–730.

Hile, R. 1936. Age and growth of the cisco *Leucichthys artedii* (LeSueur) in the lakes of northeastern highlands, Wisconsin. U.S. Bur. Fish. Bull. **48**: 211–317.

Hogman, W.J. 1970. Early scale developement on the Great Lakes coregonids, *Coregonus artedii* and *C. kiyi*. *In* Biology of coregonid fishes. *Edited by* C.C. Lindsay and C.S. Woods. University of Manitoba Press, Winnipeg. pp. 429–436.

Hurlbert, S.H. 1978. The measurement of niche overlap and some relatives. Ecology, **59**: 67–77.

Kaufman, L. 1992. Catastrophic change in species-rich freshwater ecosystems. BioScience, **42**: 846–858.

Kitchell, J.F., and Crowder, L.B. 1986. Predator–prey interactions in Lake Michigan: model predictions and recent dynamics. Environ. Biol. Fishes, **16**: 205–211.

Larkin, P.B. 1956. Interspecific competition and population control in freshwater fish. J. Fish. Res. Board Can. **13**: 327–342.

Lodge, D.M. 1993. Species invasions and deletions: community effects and responses to climate and habitat change. *In* Biotic interactions and global change. *Edited by* P.M. Karieva, J.G. Kingslover, and R.B. Heuy. Sinauer Associates, Sunderland, Mass. pp. 376–387.

Loftus, D.H., and Hulsman, P.F. 1986. Predation on larval lake whitefish (*Coregonus clupeaformis*) and lake herring (*Coregonus artedii*) by adult rainbow smelt (*Osmerus mordax*). Can. J. Fish. Aquat. Sci. **43**: 812–818.

Magnuson, J.J., Bowser, C.J., and Kratz, T.K. 1984. Long-term ecological research (LTER) on north temperate lakes of the United States. Verh. Int. Ver. Theor. Angew. Linmol. No. 22. pp. 533–535.

Magnuson, J.J., Benson, B., and McLain. A.S. 1994. Trends in species richness from long-term research. Am. Zool. **34**: 437–451.

McCauley, R.W., and Read, L.A.A. 1973. Temperature selection by juvenile and adult yellow perch (*Perca flavescens*) acclimated to 24 C. J. Fish. Res. Board Can. **30**: 1253–1255.

McLain, A.S. 1991. Conceptual and empirical analyses of biological invasion: non-native fish invasion into north temperate lakes. Ph.D. thesis, University of Wisconsin, Madison.

Moyle, P.B. 1986. Fish introductions into North America: patterns and ecological impact. *In* Ecology of biological invasions of North America and Hawaii. *Edited by* H.A. Mooney and J.A. Drake. Springer-Verlag, Berlin.

Ricker, W.E. 1958. Handbook of computations for biological statistics of fish populations. Bull. Fish. Res. Board Can. No. 119.

Schoener, T.W. 1970. Nonsynchronus spatial overlap of lizards in patchy habitats. Ecology, **51**: 408–418.

Vanderploeg, H.A., and Scavia, D. 1979. Calculation and use of selectivity coefficients of feeding: zooplankton grazing. Ecol. Modell. **7**: 135–149.

Wells, L., and McLain, A.L. 1972. Lake Michigan: effects of exploitation, introductions, and eutrophication on the salmonid community. J. Fish. Res. Board Can. **29**: 889–898.

Wismer, D.A., and Christie, A.E. 1987. Temperature relationships of Great Lakes fishes: a data compilation. Great Lakes Fish. Comm. Spec. Publ. No. 87-3.

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Improving the stock–recruitment relationship in Icelandic cod (*Gadus morhua*) by including age diversity of spawners

Gudrun Marteinsdottir and Kristjan Thorarinsson

Abstract: The size of the Icelandic cod stock has been gradually declining since the middle of this century. Recruitment has been poor over an extended period of time and much below the long-term average since 1985. Except for the concurrent decrease in stock size and recruitment during this period, the stock size – recruitment relationship is weak. This relationship is improved by including the age composition of the spawning stock. Spawning stock age diversity in each year from 1955 to 1992 was estimated with the Shannon index using the number of mature fish in each age group. By including information on age composition, 31% of the total variation in recruitment was accounted for by the model with stock size, age diversity, and the interaction between the two, compared with less than 15% by single factor models of either age diversity or stock size. These results indicate that age diversity is an important component in stock–recruitment models and that one of the management goals for fish species should be to maintain high age diversity in the spawning stocks.

Résumé : Depuis les années 50, le stock de morue d'Islande diminue progressivement. Le recrutement a été médiocre pendant une période prolongée et de beaucoup inférieur à la moyenne à long terme depuis 1985. À l'exception de la baisse concurrente de l'effectif du stock et du recrutement pendant cette période, le rapport entre l'effectif et le recrutement est faible. Ce rapport s'améliore si on inclut la composition selon l'âge du stock de géniteurs. La diversité des âges de ce stock de géniteurs pour chaque année entre 1955 et 1992 a été estimée avec l'indice de Shannon en utilisant le nombre de poissons matures dans chaque groupe d'âge. En incluant les données sur la composition selon l'âge, 31 % de la variation totale du recrutement était prise en compte par le modèle intégrant l'effectif du stock, la diversité des âges et l'interaction entre les deux, comparativement à moins de 15 % par des modèles à facteur unique utilisant la diversité des âges ou l'effectif du stock. Ces résultats montrent que la diversité des âges est une composante importante des modèles stock–recrutement; l'un des objectifs de gestion des espèces de poisson devrait être le maintien d'une grande diversité des âges dans les stocks de géniteurs.
[Traduit par la Rédaction]

Introduction

One of the central problems concerning the dynamics and management of fish populations is the apparent lack of strong stock–recruitment relationships. In general, recruitment, being itself highly variable, often appears to fluctuate independently of stock size with no relationship detected except perhaps when stock sizes are exceptionally low (Koslow 1992).

Recruitment is most often studied in relation to the size of the spawning stock, where either the number or the biomass of sexually mature individuals is assumed to represent the reproductive potential of the stock. In contrast, the age composition of the spawning stock and the effect that variable age or size structure of the stock may have on recruitment has received much less attention. The work on herring (*Clupea harengus)* by Lambert (1987, 1990) is one of the few studies that have reported on a direct relationship between age structure of a spawning population and recruitment. It was shown that better-than-average year-classes were only obtained when the age distribution of the spawning population had more than one age mode (Lambert 1990). The relationship between recruitment and the number of age modes present in the spawning population of herring was termed the "age-structured stock recruitment relationship" by Lambert (1987).

The age composition of the spawning stock is important if the different age-classes in some way contribute unequally to reproduction. A spawning stock with diverse age structure may result in a broader spatial and temporal distribution of spawning, resulting from size- or age-dependent timing, duration, or location of spawning (as described for cod (*Gadus morhua*) by Hutchings and Myers (1993) and Marteinsdottir and Petursdottir (1995)), thus enhancing the probability of larvae finding favorable environmental conditions (Rothschild 1986). Unequal contributions of separate age-classes may also result from differential numbers of offspring produced by each age-class or by variable survival of eggs and larvae due to quality differences of offspring produced by females of different ages, sizes, and conditions (Hislop 1988; Solemdal et al. 1995; Marteinsdottir and Steinarsson 1998).

As with many other fish stocks, the Icelandic cod stock exhibits weak and uncertain stock–recruitment relationship (Baldursson et al. 1996). From the middle of this century, the spawning stock biomass gradually declined from 1.4×10^6 t towards historical low levels at approximately 200 000 t in 1988 and 1993 (Schopka 1994; Anonymous 1997). Along with decreasing stock size the recruitment also declined drastically.

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Recruitment has been low or exceptionally low since 1985, compared with the 1955–1992 average of 205 ×106 3-year-old cod (Anonymous 1997). Furthermore, since the middle of this century, the time interval between strong year-classes has increased, and below-average recruitment has been observed more and more frequently. Although the declines in stock size and recruitment coincide, the relationship between recruitment and spawning stock biomass is weak and strong year-classes have been generated during periods of exceptionally low stock sizes, as in 1973 and 1983–1984 when some of the largest cohorts on record were produced.

The present paper focuses on the combined influence of both stock age structure and stock size on recruitment in Icelandic cod. The main objective is to examine whether the relationship between stock size and recruitment can be improved by including information on the age composition of the stock.

Materials and methods

The age composition of the spawning stock of Icelandic cod was calculated from stock size in numbers at age and the estimated proportions sexually mature at age (Stefansson 1992; Anonymous 1996). Recruitment numbers (number of 3 year olds) and spawning stock biomass were obtained from a virtual population analysis presented in Anonymous (1996).

The diversity of the age structure of the spawning stock in each year was estimated with the Shannon diversity index (Shannon 1948). The Shannon diversity index was employed to obtain a single value, independent of stock size, that described both the number of cohorts in the stock and the evenness of the distribution of fish among cohorts. The index is defined as

$$(1) \qquad H = (n\log(n) - \sum_{i=1}^{k} f_i \log(f_i))/n$$

The logarithmic base of 10 was used to compute H, where k is the number of age groups, n is the total number of mature fish in all age groups, and f_i is the number of mature fish in each age group. The calculated index value depends on the distribution of the data as well as the number of categories (age groups) present; the maximum diversity for a set of data, consisting of k categories, is equal to $\log(k)$ (Zar 1974).

A multiple linear regression model (Neter et al. 1985) was used to describe the combined effects of spawning stock biomass (SSB) and age diversity (H) on recruitment (R):

$$(2) \qquad R_i = \alpha + \beta_1 H_i + \beta_2 \log_e(\mathrm{SSB}_i) + \beta_3 (H_i \log_e(\mathrm{SSB}_i)) + \varepsilon_i$$

where $\varepsilon_i \sim N(0, \sigma^2)$. The response variable, R, was transformed to achieve normality of residuals; transformations of the form $R' = R^p$ with $p = \{2, 1, 0.5, -0.5, -1, -2\}$, were tried, as was $R' = \log_e(R)$. The residuals from each regression were tested for normality by converting to normal scores and computing the correlation between the residuals and their normal scores (Anonymous 1989).

Results

Diversity in age composition

Along with a steady decline in the size of the spawning stock since the middle of the century (Fig. 1*a*), the general age composition has changed as well (Figs. 1*c* and 2). During the 1950s and 1960s, with relatively high stock levels, the age composition was diverse. At least two or three strong year-classes were present at each time, and these year-classes reached old age before they disappeared from the stock. In more recent years, periods of narrow age distributions have become more frequent (Fig. 1*c*), and fewer fish survive beyond the age of 7 or 8 years (Fig. 2). The Shannon index describes these differences, being generally larger in the years 1955–1962 than during any later time periods (Fig. 1*c*, Table 1). In addition, the lowest values of the index were all obtained after 1975, expressed by strikingly narrow age distributions in 1979, 1989, and 1990.

The stock–recruitment relationship

A relatively large proportion of the variation in recruitment was explained by including information on both stock size and age diversity in the model. The most successful transformations ($-\log_e R$, $-1/R^{0.5}$, and $-1/R$) resulted in residuals that did not deviate significantly from normality ($\alpha = 0.01$). Of these, the transformation $R' = -1/R$ was chosen based on considerations of symmetry of residuals. The relationship between recruitment and spawning stock variables, size and age composition, may therefore be given as

$$-1/R = -0.143 + 0.158H + 0.0215 \log_e \mathrm{SSB} - 0.0246H\log_e \mathrm{SSB}$$

All parameters in the model have a significant contribution ($p < 0.05$) and the overall F test for the model is highly significant ($p < 0.01$).

The model accounts for 30.5% of the variation in recruitment (coefficient of determination, $R^2 = 0.305$). This is a considerable improvement over simple regression models with either spawning stock biomass ($\log_e(\mathrm{SSB})$) or age diversity (H) as the predictor, the simple models never accounting for more than 15% of the recruitment variation (Fig. 3).

The interaction term between H and SSB was significant ($p < 0.05$). This negative interaction indicates that recruitment will increase with increasing age diversity up to a certain size of the spawning stock after which the effects of age diversity are less important.

Discussion

Like many other fish stocks, the Icelandic cod stock exhibits a weak stock size–recruitment relationship (summarized by Myers et al. 1995). The present paper shows that this relationship may be improved by including information on age composition in the model. Therefore, when searching for such relationships it may be important to regard the spawning stocks not as single entities with respect to their sizes but rather as being composed of individuals of various sizes and ages, which may contribute differently toward the reproduction.

In the Icelandic cod stock, the poor relationship between recruitment and stock size has made it difficult to detect recruitment overfishing and thus to demonstrate the importance of maintaining the spawning stock above a certain minimum level. The present analysis indicates that stock attributes may have a marked effect on recruitment.

Spawning stock size and age diversity

The importance of stock size is clearly seen when one considers the connection between stock size and age composition. The age composition is influenced by the recruitment of strong year-classes into the spawning stock. Therefore, as the size of the Shannon index, representing age diversity, is determined

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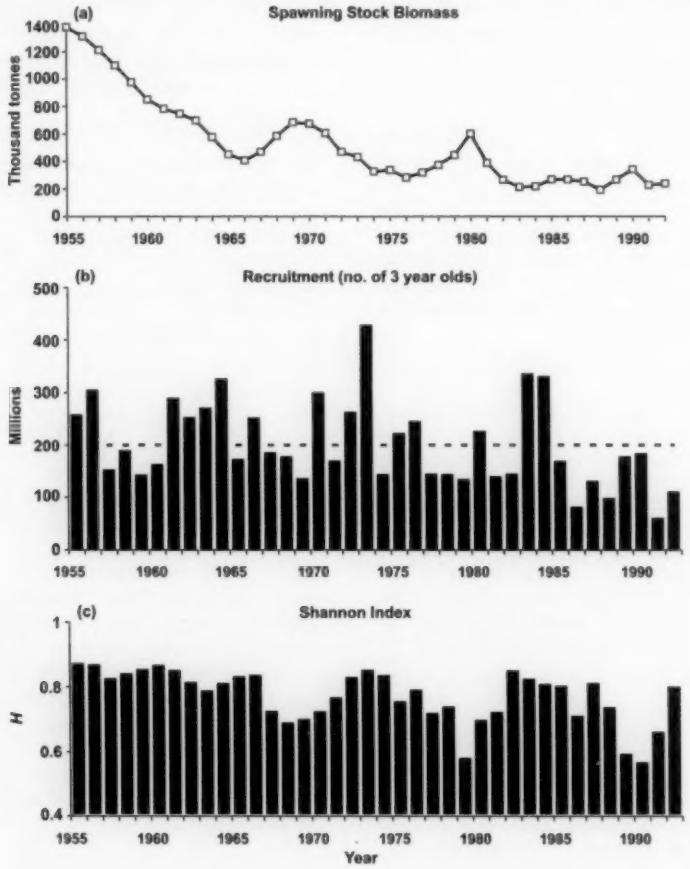
Fig. 1. Attributes of the Icelandic cod stock in 1955–1992: (*a*) spawning stock biomass and (*b*) recruitment for the same period, presented as the number of 3 year olds, and (*c*) age diversity represented by Shannon index values (*H*). The broken line shows the average recruitment during 1955–1992.



by the number and relative strength of the age groups present, the index will increase when strong year-classes progress through time and attain relatively high age, and thus increase numbers and sizes in the older age groups. On the other hand, the peak in spawning stock biomass occurs a few years prior to maximum age diversity (Fig. 1*a*), i.e., at the time when members of large year-classes have already entered the spawning stock, increased in weight, yet are still present in relatively high numbers. As an example, the strong year-class of 1973 was recruited into the spawning population at the age of 3–5 years during 1976–1978. However, it is not until 1979–1980, when the members of this cohort are 6 or 7 years old, that they begin to have significant impact on the spawning stock biomass. At the same time, age diversity (Shannon index in Fig. 1*c*) is low because the age structure is mostly limited to 6- and 7-year-old fish. It is not until a few years later (in 1983–1984), when these fish attain older age (10–12 years old), that the age diversity increases. The two strong year-classes of 1983 and 1984 are generated during this period of high age diversity.

A significant reduction in the size of strong year classes a few years after they enter the spawning stock (i.e., at the age of 5–7 years), because of high fishing mortality, may result in continuing low recruitment. In the Icelandic cod stock, peaks in spawning stock size have gradually become smaller since the middle of the century (Fig. 1*a*). This reflects increasing fishing pressures. Actually, fishing pressure on the large 1983–1984 year-classes was so intensive that the contribution of these year classes to spawning stock biomass at age 6 or 7 in 1990–1991 was only a fraction of the contribution of the 1973 year-class in 1980 (Fig. 1*a*). Consequently relatively few members of the 1983–1984 year-classes survived to the age of 10 or 11, e.g., the age necessary to promote increased age diversity in 1993 and 1994. In concordance, estimated values for the Shannon Index in 1993 and 1994 were only 0.71 and 0.61, compared with higher index values in 1973 ($H = 0.86$) and 1983 ($H = 0.83$) when the two largest year-classes in this study were spawned. Estimates of recruitment also indicate that the 1993 and 1994 year-classes will be near and below average, respectively (Anonymous 1997).

In general, changes in age distributions of spawning stocks are likely to follow declining stock levels. Excessive removal of older individuals from the stocks will lead to narrow age distributions and, as summarized by Tripple et al. (1997),

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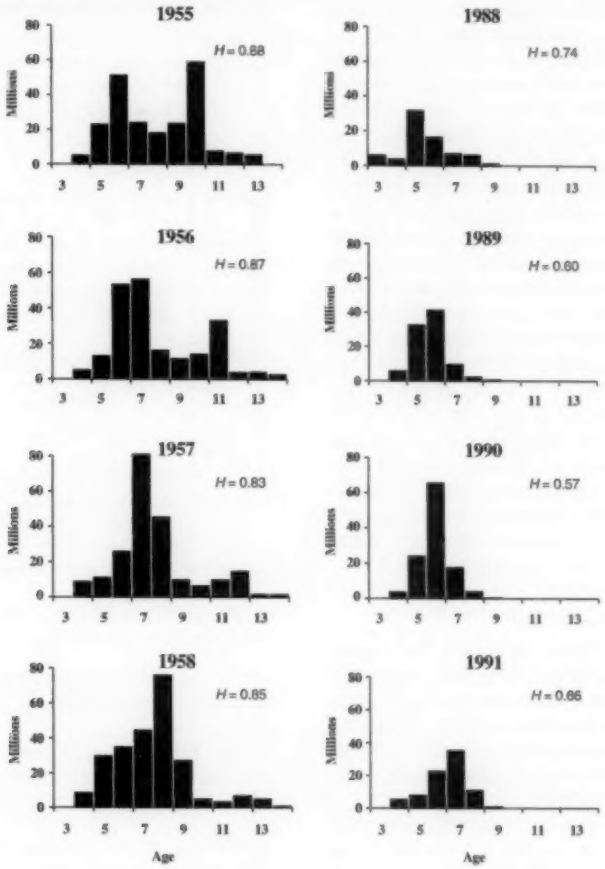
Fig. 2. Age distribution of the spawning stock of Icelandic cod during high stock levels in 1955–1958 and low stock levels in 1988–1991, showing the values of the Shannon index (H) for each of the years.



depletion of older individuals from various fish stock has been associated with periods of stock decline. Although manifestly common among many stocks, few other studies have reported on changes in stock compositions in association with high exploitation rates. The present study provides a simple tool to explore age diversity and changes in age distributions.

Table 1. Comparisons of mean Shannon index in four time periods since 1955.

Time period	Mean Shannon index $F_{3,37} = 3.94$; $p = 0.02$
1955–1962	$0.86 \pm 0.02a$
1963–1972	$0.78 \pm 0.06b$
1973–1982	$0.76 \pm 0.08b$
1983–1992	$0.74 \pm 0.09b$

Note: Time periods were determined arbitrarily at 10-year intervals counting backwards from 1992. Therefore, the earliest group (1955–1962) in that series consisted of only 8 years. Shannon indices were compared using ANOVA and a Student–Newman–Keuls multiple comparisons test; values with the same letter were not significantly different from each other at $\alpha = 0.05$.

"Bet hedging" and the duration of spawning

Further information on how the age composition affects recruitment is needed. Increased diversity in age composition may result in greater spread of spawning, both temporally and spatially, brought about by the greater number of age-classes initiating spawning at different times as well as in extended spawning areas at high levels of stock abundance. Protracted spawning is believed to enhance offspring survival by allowing the stock to "hedge its bet" against adverse environmental conditions (Murphy 1968; Stearns 1976; Legget and Carscadden 1978; Roff 1978, 1981). Thus, variable recruitment in the Norwegian spring spawning herring (*Clupea harengus*) has been associated with variation in the duration and distribution of spawning (Dragesund 1970). Thus recruitment variability may in part reflect variation in the age-class composition of the spawning stock (Lambert 1987, 1990) where the number of discrete spawning events (spawning waves of distinct age and size groups) corresponds to the number of dominant age groups or peaks in the age distribution at each time. It was shown that above-average recruitment was only obtained when the population was composed of more than two age

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modes (Lambert 1990). Variation in spawning time that can be related to the age composition of the spawning stock has also been established for cod both in the Northwest Atlantic and in Icelandic waters. In the Newfoundland–Labrador region, younger cod started spawning earlier than older cod, which in turn completed spawning later in the season than the younger ones (Hutchings and Myers 1993). In contrast, larger females in the Icelandic cod stock started spawning much earlier than the smaller ones (Marteinsdottir and Petursdottir 1995). The same study showed that the end of spawning among the large and small females occurred at a similar time in 1994, while in 1995 the smaller females appeared to complete spawning later in the season than the larger ones. In both of these studies on the Northwest Atlantic and the Icelandic cod, duration of spawning was shown to increase with age or size. In the Icelandic cod stock, larger cod females were shown to spawn over a time period that was, in some cases, 4–5 weeks longer than the spawning period of the smaller females. However, the spawning time of the younger fish is not overlapped completely by the spawning time of the older fish, e.g., earlier start of younger cod in Newfoundland and in some years a later seasonal spawning of younger and smaller cod in Icelandic waters (Hutchings and Myers 1993; Marteinsdottir and Petursdottir 1995). Therefore, increases in the numbers of younger cod may also increases the duration of spawning.

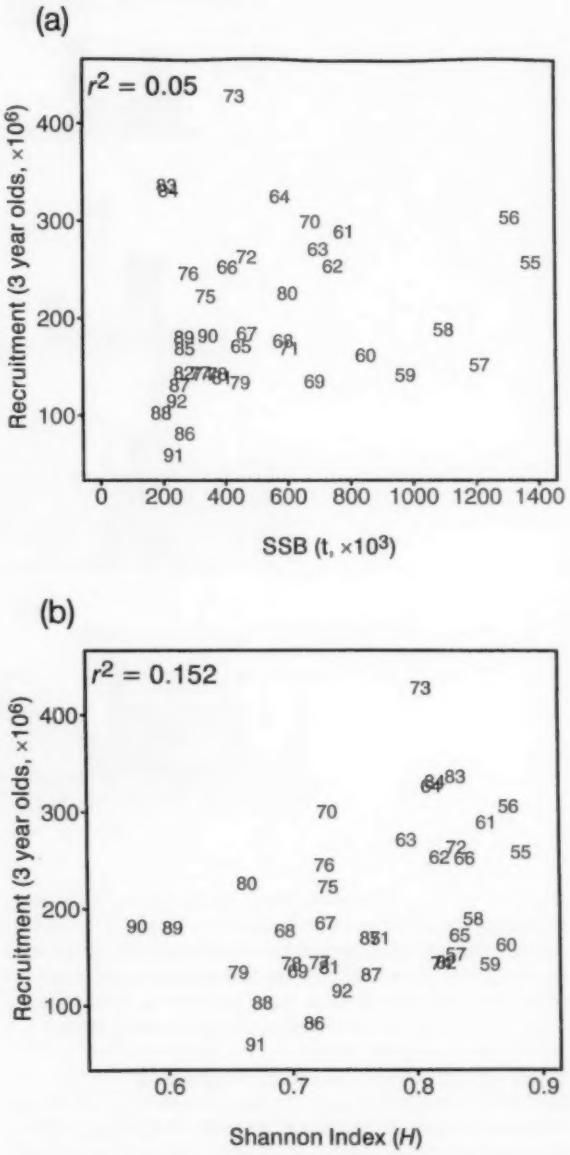
Age- or size-dependent egg production

An increase in the proportion of older individuals in the stock may also result in improved recruitment resulting from greater contribution of older individuals to the reproduction brought about by the higher fecundity and greater viability of eggs and larvae produced by older or larger females. Variation in fecundity has been most often related to food supplies and the nutritional status of the females (Rothschild 1986; Bagenal 1973). In addition, many studies have shown that relative fecundity increases with age, body size, or condition (DeMartini and Fountain 1981, and references therein; Hislop 1988; Kjesbu et al. 1991; Rijnsdorp et al. 1991), indicating that larger females do on the average produce a relatively greater number of eggs.

Although numerous studies have demonstrated the positive relationship between female size, egg size, and larval size (Blaxter and Hempel 1963; Hempel and Blaxter 1967; Pitman 1979; Marteinsdottir and Able 1984, 1992; Springate and Bromage 1985; Kazakov 1981; Knutsen and Tilseth 1985; Kjesbu et al. 1996; Tripple et al. 1997; Marteinsdottir and Steinarsson 1998), it has proved difficult to demonstrate that maternal effects actually influence the survival of larvae or juveniles in nature (Leggett and DeBlois 1995; Chambers and Legget 1996). However, a relationship between female size and egg survival has been established for cod (Solemdal et al. 1995). Solemdal et al. (1995) showed that eggs produced by females held in captivity over several consecutive years exhibited less mortality during incubation as the females grew older. Cod larvae from larger eggs grow faster during the first 2 weeks (Marteinsdottir and Steinarsson 1998), while surviving cod juveniles with faster growth also had larger otolith hatch marks than the initial general population (Meekhan and Fortier 1996), thus connecting survival with a trait already present at hatching.

The present study demonstrates that both size and age composition of the spawning stock influence recruitment. The mechanism by which changing age composition affects recruitment is likely to consist of multiple age- or size-specific components including fecundity and maternal effects, as well as spatial and temporal variation in timing and duration of spawning. The importance of each component may vary from one year to another, depending on the interplay with environmental factors such as the timing of the production cycle. Thus, the goal of fishery management should be to conserve reproductive potential by maintaining high age diversity in the spawning stock as well as adequate stock size to facilitate production of large year-classes.

Fig. 3. Scatterplots showing the relationship between (*a*) spawning stock biomass (SSB) and recruitment and (*b*) age diversity (Shannon index) and recruitment.



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References

Anonymous. 1989. MINITAB reference manual, release 7. Minitab, Inc., State College, Pa.

Anonymous. 1996. State of marine stocks in Icelandic waters 1995/96. Prospects for the quota year 1996/97. Mar. Res. Inst. Ser. No. 43. (Available upon request from the Library of the Marine Research Institute, Skulagata 4, P.O.Box. 1390, 121 Reykjavik, Iceland.)

Anonymous. 1997. State of marine stocks in Icelandic waters 1996/97. Prospects for the quota year 1997/98. Mar. Res. Inst. Ser. No. 43. (Available upon request from the Library of the Marine Research Institute, Skulagata 4, P.O.Box. 1390, 121 Reykjavik, Iceland.)

Bagenal, T.B. 1973. Fish fecundity and its relations with stock and recruitment. Rapp. P.-V. Réun. Cons. Int. Explor. Mer, **164**: 186–198.

Baldursson, F.M., Danielsson, A., and Stefansson, G. 1996. On the rational utilization of the Icelandic cod stock. ICES J. Mar. Sci. **53**: 643–658

Blaxter, J.H.S., and Hempel, G. 1963. The influence of egg size on herring larvae (*Clupea harengus* L.). J. Cons. Cons. Int. Explor. Mer, **28**: 211–240.

Chambers, R.C., and Leggett, W.C. 1996. Maternal influence on variation in egg size in temperate marine fishes. Am. Zool. **36**: 180–196.

DeMartini, E.E., and Fountain, R.K. 1981. Ovarian cycling frequency and batch fecundity in the queenfish, *Seriphus politus*: attributes representative of serial spawning fishes. Fish. Bull. U.S. **79**: 547–560

Dragesund, O. 1970. Factors influencing year-class strength of Norwegian spring spawning herring (*Clupea harengus* Linne). Fiskeridir. Skr. Ser. Havunders. No. 15. pp. 381–450.

Hempel, G., and Blaxter, J.H.S. 1967. Egg weight in Atlantic herring (*Clupea harengus* L.). J. Cons. Cons. Int. Explor. Mer, **31**: 170–195.

Hislop, J.R.G. 1988. The influence of maternal length and age on the size and weight of the eggs and the relative fecundity of the haddock, *Melanogrammus aeglefinus*, in British waters. J. Fish. Biol. **32**: 923–930.

Hutchings, J.A., and Myers, R.A. 1993. Effect of age on the seasonality of maturation and spawning of Atlantic cod, *Gadus morhua*, in the Northwest Atlantic. Can. J. Fish. Aquat. Sci. **50**: 2468–2474.

Kazakov, R.V. 1981. The effect of the size of Atlantic salmon, *Salmo salar* L., eggs on embryos and alevins. J. Fish. Biol. **19**: 353–360.

Kjesbu, O.S., Klungsöyr, J., Kryvi, H., Witthames, P.R., and Greer Walker, M. 1991. Fecundity, atresia, and egg size of captive Atlantic cod (*Gadus morhua*) in relation to proximate body composition. Can. J. Fish. Aquat. Sci. **48**: 2333–2343.

Kjesbu, O.S., Solemdal, P., Bratland, P., and Fonn, M. 1996. Variation in annual egg production in individual captive Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **53**: 610–620.

Knutsen, G.M., and Tilseth, S. 1985. Growth, development, and feeding success of Atlantic cod (*Gadus morhua*) larvae related to egg size. Trans. Am. Fish. Soc. **114**: 507–511.

Koslow, J.A. 1992. Fecundity and the stock–recruitment relationship. Can. J. Fish. Aquat. Sci. **49**: 210–217.

Lambert, T.C. 1987. Duration and intensity of spawning in herring *Clupea harengus* as related to the age structure of the mature population. Mar. Ecol. Prog. Ser. **39**: 209–220.

Lambert, T.C. 1990. The effect of population structure on recruitment in herring. J. Cons. Cons. Int. Explor. Mer, **47**: 249–255.

Leggett, W.C., and Carscadden, J.E. 1978. Latitudinal variation in reproductive characteristics of American shad (*Alosa sapidissima*): evidence for population specific life history strategies in fish. J. Fish. Res. Board Can. **35**: 1469–1478.

Leggett, W.C., and DeBlois, E. 1995. Researching recruitment—where to now? Mar. Ecol. Prog. Ser. **128**: 305–310.

Marteinsdottir, G., and Able, K.W. 1984. Geographic variation in egg size among populations of the mummichog, *Fundulus heteroclitus* (Pisces: Fundulidae). Copeia, 1984: 471–478.

Marteinsdottir, G., and Able, K.W. 1992. Influence of egg size on embryos and larvae of *Fundulus heteroclitus* (L.). J. Fish. Biol. **41**: 883–896.

Marteinsdottir, G., and Petursdottir, G. 1995. Spatial and temporal variation in reproduction of Icelandic cod at Selvogsbanki and nearby coastal areas. ICES CM 1995/G:15

Marteinsdottir, G., and Steinarsson, A. 1998. Maternal influence on the size and viability of cod (*Gadus morhua* L.) eggs and larvae. J. Fish Biol. **52**: 1241–1258.

Meekan, M.G., and Fortier, L.1996. Selection for faster growth during the larval life of Atlantic cod *Gadus morhua* on the Scotian Shelf. Mar. Ecol. Prog. Ser. **137**: 25–37.

Murphy, G.I. 1968. Pattern in life history and the environment. Am. Nat. **102**: 391–403.

Myers, R.A., Bridson, J., Barrowman, N.J. 1995. Summary of worldwide stock and recruitment data. Can. Tech. Rep. Fish. Aquat. Sci. No. 2024.

Neter, J.,Wasserman, W., and Kutner, M.H. 1985. Applied linear statistical models. 2nd ed. Richard D. Irwin, Inc., Homewood, Ill.

Pitman, R.W. 1979. Effects of female age and egg size on growth and mortality in rainbow trout. Prog. Fish-Cult. **41**: 202–204.

Rijnsdorp, A.D., Daan, N., Feek, F.A., and Heessen, H.J.L. 1991. Reproductive variability in North Sea Plaice, sole and cod. J. Cons. Cons. Int. Explor. Mer, **47**: 352–375.

Roff, D.A. 1978. Size and survival in stochastic environment. Oecologia, **36**: 163–172.

Roff, D.A. 1981. Reproductive uncertainty and the evolution of iteroparity: why don't flatfish put all their eggs in one basket? Can. J. Fish. Aquat. Sci. **38**: 968–977.

Rothschild, B.J. 1986. Dynamics of marine fish populations. Harvard University Press, Cambridge, Mass., London.

Schopka, S.A. 1994. Fluctuations in the cod stock at Iceland during the twentieth century in relation to changes in the fisheries and environment. ICES Mar Sci. Symp. **198**: 175–193.

Shannon, C.E. 1948. A mathematical theory of communication. Bell Syst. Tech. J. **27**: 379–423.

Solemdal, P., Kjesbu, O., and Fonn, M. 1995. Egg mortality in recruit- and repeat-spawning—an experimental study. ICES CM 1995/G:35.

Springate, J.R.C., and Bromage, N.R. 1985. Effects of egg size on early growth and survival in rainbow trout (*Salmo gairdneri* Richardson). Aquaculture, **47**: 163–172.

Stearns, S.C. 1976. Life history tactics: a review of the ideas. Q. Rev. Biol. **51**: 3–47.

Stefansson, G. 1992. Notes on the stock-dynamics and assessments of the Icelandic cod. ICES C.M. 1992/G:71.

Tripple, E.A., Kjesbu, O.S., and Solemdal, P. 1997. Effects of adult age and size structure on reproductive output in marine fishes. *In* Early life history and recruitment in fish populations. *Edited by* R.C. Chambers and E.A. Tripple. Chapman & Hall, London. pp. 31–62.

Zar, J.H. 1974. Biostatistical analysis. Prentice-Hall, Engelwood Cliffs, N.J.

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Dietary effects on the fatty acid signature of whole Atlantic cod (*Gadus morhua*)

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Abstract: Understanding the influence of dietary fatty acids on whole fish is necessary to evaluate the degree to which fatty acids may be used for understanding foraging patterns in fish, as well as in marine mammals that consume their prey whole. Adult Atlantic cod (*Gadus morhua*) were fed two prey items that differed significantly in fat content and fatty acid compositions. Cod were first fed squid (*Illex illecebrosus*, 2.0% fat) for 6 weeks, followed by Atlantic mackerel (*Scomber scombrus*, 15.7% fat) for 8 weeks. Twenty whole cod were individually analyzed at each of 0, 3, 6, 11, and 14 weeks. Despite being on a low-fat squid diet, in only 3 weeks, cod fatty acid patterns changed significantly to reflect the patterns found in squid and did not further change at 6 weeks. When switched to a high-fat mackerel diet, total body fat of cod increased and the fatty acid composition of cod changed significantly in the direction of patterns found in mackerel. Despite changes in cod fatty acid signatures, cod were readily distinguished from the fatty acid signatures of their diets. Our results provide support for the use of fatty acids as indicators of diet at upper trophic levels.

Résumé : On doit connaître l'influence des acides gras alimentaires sur le poisson entier pour établir dans quelle mesure les acides gras peuvent être utilisés pour comprendre les comportements de recherche de nourriture des poissons et des mammifères marins qui consomment leurs proies entières. On a nourri des morues (*Gadus morhua*) adultes avec deux types de proie dont les teneurs en gras et les compositions en acides gras différaient significativement. Les morues ont d'abord consommé du calmar (*Illex illecebrosus*, 2,0 % de matières grasses) durant 6 semaines, puis du maquereau (*Scomber scombrus*, 15,7 % de matières grasses) durant 8 semaines. Vingt morues entières ont été individuellement analysées à chacune des étapes suivantes : 0, 3, 6, 11 et 14 semaines. Bien que les morues aient été exposées à un régime de calmar faible en matières grasses, en seulement 3 semaines, les profils d'acides gras des morues ont changé significativement pour refléter ceux du calmar, et ils étaient les mêmes à 6 semaines qu'à 3 semaines. Quand les morues sont passées au régime de maquereau riche en matières grasses, leur teneur corporelle totale en matières grasses s'est accrue et leur composition en acides gras a changé significativement pour s'approcher de celle du maquereau. Malgré les changements dans les profils d'acides gras de la morue, ces derniers demeuraient nettement distincts des profils d'acides gras de ses proies. Nos résultats indiquent qu'il est possible d'utiliser les acides gras comme indicateurs du régime alimentaire dans les niveaux trophiques supérieurs.
[Traduit par la Rédaction]

Introduction

The concept of using lipids as biomarkers in marine ecosystems has received considerable attention in the past few decades (e.g., Sargent et al. 1988). Some of the first evidence for the conservative transfer of these fatty acids in neutral lipids came from experiments on phytoplankton and copepods (Lee et al. 1971), and tracer lipids in plankton continue to be the most studied. For example, diatoms contain high levels of 20:5*n*–3 whereas dinoflagellates are rich in 22:6*n*–3, green algae in 18:4*n*–3, and red algae in 20:4*n*–6 (Sargent 1989). Recently, there has been growing interest in the use of fatty acids to examine the foraging ecology and diet of a wider variety of marine species, including those of higher trophic levels. Kharlamenko et al. (1995) used long-chain fatty acids, unique to bacteria and algae, to determine food sources of macrozoobenthic species in a shallow-water hydrothermal ecosystem. Similarly, diet information was gained from studying the transfer of the fatty acid 18:2*n*–6 (Klungsøyr et al. 1989), or the ratio of 16:1*n*–7 to 16:0 (St. John and Lund 1996), from diatoms to copepods and on to larval Atlantic cod (*Gadus morhua*). Sargent (1989) reported that zooplanktivorous fish, caught during the spring and autumn algal blooms, had large amounts of the fatty acids 20:1*n*–9 and 22:1*n*–11, which corresponded to the fatty alcohol of the wax esters laid down by the copepods feeding on the algae. These zooplanktivorous fish are consumed in turn by other commercially important fish species such as cod, haddock (*Melanogrammus aeglefinus*), and pollock (*Pollachius virens*). Hence, the livers of these piscivorous fishes were found to be rich in 20:1*n*–9 and 22:1*n*–11 and also contained high levels of the *n*–3 polyunsaturated fatty acids (Sargent 1989), which were characteristic of the phytoplankton.

Several studies have examined the fatty acid patterns at yet higher trophic levels, such as in the milks and blubber from various marine mammals, in relation to dietary intake

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(reviewed in Iverson 1993). For instance, Antarctic fin whales (*Balaenoptera physalus*), whose diet consists primarily of herbivorous euphausiids, and North Atlantic fin whales, who feed on zooplankton, were easily differentiated by levels of 20:1 and 22:1 which were characteristic of their prey (Ackman and Eaton 1966). Similarly, populations of freshwater and saltwater harbour seals (*Phoca vitulina*) in northern Quebec could be distinguished using stable-isotope ratios and dietary fatty acids (Smith et al. 1996). More recently, fatty acids have been used to study the spatial scales of foraging and temporal variations in diets of other pinnipeds (Iverson et al. 1997*a*, 1997*b*).

It is well established in various fish species that the fatty acid composition of diet influences the lipid composition of tissues such as liver and muscle (Cowey and Sargent 1972; Yu et al. 1977; Lie et al. 1986; Nelson 1992; Dos Santos et al. 1993; Xu et al. 1993). Indeed, because the liver is the primary site of lipid deposition and storage in fish, it has been the tissue most frequently studied. However, higher trophic level predators including seals and other marine mammals generally consume their prey whole. Thus, to use fatty acids as an ecological tool, we must understand the influence of diet on the fatty acid signature of the whole body, rather than on individual fish tissues. Additionally, it may be the entire array of fatty acids in a species (i.e., the "signature," Iverson 1993; Iverson et al. 1997*b*), rather than the few selected components, that are the focus in biomarker studies, which will eventually allow quantitative assessments of diets.

Our study had two objectives within a larger program on the development of fatty acid signature analysis. Our first aim was to determine whether the fatty acid signature of whole cod changes with a change in diet, whether these changes reflect the fatty acid signatures of the prey being consumed, and finally what kind of time course would be required for such changes to occur. This information would provide the opportunity to use fatty acids to study the foraging ecology of fish predators as well as marine mammal predators. Fatty acid signatures of whole Atlantic cod are of particular interest, as this species is both commercially important and believed to be a significant prey of seals in Atlantic Canada (e.g., Bowen and Harrison 1994). Our second objective was to determine the stability of the cod fatty acid signatures by statistically comparing cod on dietary treatments with signatures of their experimental prey and with that of wild cod, i.e., can a cod still be identified as a cod by its fatty acid signature despite changes in and influences by diet. If fatty acids are to be used to study the foraging ecology of seals, it is important to establish the ability to distinguish all prey based on their fatty acid compositions despite the influence of diet on those compositions.

Materials and methods

Maintenance and experimental design

In December 1993, about 100 large adult Atlantic cod (47.4 ± 0.63 cm, 1.0 ± 0.04 kg) were captured by bottom trawl near Devil's Island, Eastern Passage, Dartmouth, N.S. The cod were housed in four flow-through tanks (6 m^3) to maintain them at a density that favours increased survival and appetite. Lighting was controlled to simulate the seasonal photoperiod. Temperature of the filtered seawater (31‰) delivered to the tanks varied seasonally (December to mid-April, 0.3–4.0°C). During the experiment, cod were fed every second day ad libitum, as Dos Santos et al. (1993) reported that cod fed at a reduced frequency showed greater growth rates and food utilization than cod fed daily. We had no a priori reason to expect large changes in fatty acids in these nonreproducing fish over the duration of the experiment if on a constant diet. Thus, cod were randomly divided into groups of equal size for diet treatments and sampling. Because the time of the study coincided with greatly reduced availability of wild cod for use in our study, the experiment was set up as a basic intervention design to maximize the number of cod that were analyzed for changes in fatty acid composition at each time period. There were a total of five sampling periods, and at each sampling, five cod were randomly selected from each tank for analysis.

To establish a baseline signature of the wild cod during acclimation to our facilities, they were fed other cod from the same net haul for the first 4 weeks, after which the first set of cod samples (CodC, week 0, $N = 20$) were obtained for proximate and fatty acid analysis. Cod were then fed squid (*Illex illecebrosus*, 2% lipid), cut into 5- to 8-cm strips, for 6 weeks. Cod were sampled at 3 weeks (CodS1, $N = 20$) and 6 weeks (CodS2, $N = 20$) after the start of the squid diet. During these two 3-week periods, tank water temperatures averaged 4.0 and 2.8°C, respectively. The cod were then switched to a diet of Atlantic mackerel (*Scomber scombrus*, 16% lipid), cut into 5- to 8-cm pieces with the heads, tails, and viscera removed, for 8 weeks. This second diet was fed slightly longer due to a significant reduction in food consumption that coincided with lower water tempertaures during the final two periods (1.7 and 2.3°C, respectively). The cod on the mackerel diet were sampled at 5 weeks (CodM1, $N = 20$) and 8 weeks (CodM2, $N = 24$, all remaining cod in the tanks) after the start of the mackerel diet. All squid and mackerel fed to the cod were purchased from the same vendor at the same time.

At each sampling the cod were killed by placing them in a bath containing lethal concentrations of tricainemethanesulfonate (MS 222) and stored for several weeks in sealed plastic bags at –20°C until processing. Samples of the diet (18 squid and 25 mackerel in total) were taken at each feeding and frozen for subsequent proximate and fatty acid composition analysis. The squid and mackerel taken for analysis were treated the same way as those fed to the cod.

Laboratory and data analysis

Cod and prey samples were thawed and individually ground and analyzed for dry matter (by forced convection at 100°C for about 5 h), protein (by the Kjeldahl method, Bradstreet 1965), fat (Bligh and Dyer 1959), and fatty acid composition. Fatty acid methyl esters were prepared from the lipid extract (filtered and dried over anhydrous sodium sulfate), using 8% boron trifluoride in methanol (v/v) and hexane, capped under nitrogen gas, and heated at 100°C for 1 h. Using fresh reagents, this method produces results identical to those using 0.5 N sulfuric acid in methanol (Iverson 1988; Iverson et al. 1997*b*). Fatty acid methyl esters were analyzed in duplicate using temperature-programmed capillary gas–liquid chromatography (GLC) according to Iverson (1988) and Iverson et al. (1992), but on a Perkin Elmer (PE) Autosystem II Capillary FID gas chromatograph fitted with a 30 m × 0.25 mm inside diameter column coated with 50% cyanopropyl polysiloxane (0.25 film thickness, J&W DB-23, Folsom, Calif.) and linked to a computerized integration system (PE Nelson). Fatty acids were identified and quantified according to Iverson et al. (1997*b*) using a combination of standard mixtures (Nu-Chek-Prep, Inc., Elysian, Minn.) and silver nitrate chromatography, as well as an ion-trap mass spectrometer (R.G. Ackman, personal communication). The fatty acids are designated in IUPAC nomenclature by carbon chain length:number of double bonds and the position (n–x) of the first double bond with respect to the methyl end. Seventy-two fatty acids and isomers were regularly identified in all cod and prey samples. Additionally, isomers (n–11 and n–9) of two long-chain monounsaturated fatty acids, 20:1 and 22:1, and the ratio of these isomers have been found to be good indicators of diet (Iverson 1993; Iverson et al.1997*b*). Thus, ratios of 20:1n–11/20:1n–9 (ratio 20:1)

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and 22:1*n*–11/22:1*n*–9 (ratio 22:1) were also included in the fatty acid data sets for analysis. Data are presented as mean ± SEM.

Cod treatment comparisons, as well as any between-tank differences, were tested using two-way multivariate analysis of variance (MANOVA) on arcsin-transformed fatty acid data. To perform MANOVA, four cod were randomly removed from the final sampling period to create equal sample sizes for all sampling periods. Because of the group sample size ($N = 20$), up to 19 fatty acids could be used for this statistical analysis. Therefore, this data set consisted of the 18 fatty acids and one isomer ratio, which were either present at the most abundant levels and (or) were relevant to dietary differences (Table 1). One-way ANOVA was used to compare fat content and selected individual fatty acids of prey and cod.

To examine the overall differences in cod signatures with diet, all fatty acids were analyzed using classification and regression tree (CART) analysis in S-plus (Statistical Sciences Inc., Seattle, Wash.) according to Smith et al. (1997) and Iverson et al. (1997*a*). CART is a nonparametric multivariate classification technique that enables the statistical interpretation of fatty acid patterns containing a high number of variables (fatty acids) per observation. CART sequentially selects the "best" variable, and the best splitting point of that variable, to separate the data into two groups (nodes) that are as different as possible. This splitting continues until one of two stopping criteria (based on deviance and number of observations) is met and a classification is made along with the associated misclassification or error rate. We also used deviances of other fatty acids calculated in the CART analysis to determine other fatty acids that could be used for the initial split at the root node (Clark and Pregibon 1992; Venables and Ripley 1994). Although CART compares quite favourably with more traditional multivariate techniques, such as discriminant function analysis, CART may be advantageous because subjective variable selection is not required when the number of fatty acids exceeds the number of samples (Smith et al. 1997).

Results

Prey composition

The total fat and fatty acid compositions of the prey species fed to the cod differed considerably. The fat content of squid averaged 2.0% (CV = 45.6%) compared with 15.8% fat (CV = 19.4%) in mackerel ($P < 0.0001$) (Table 1). The percentage of many of the major fatty acids also differed significantly. Squid and mackerel fatty acid signatures differed based on the 18 fatty acids and one isomer ratio (MANOVA, $P < 0.0001$) (Table 1). For example, squid contained high levels of 20:4*n*–6, 20:5*n*–3, and 22:6*n*–3 (1.52, 12.93, and 33.77%, respectively) compared with much lower levels of these components in mackerel (0.44, 7.54, and 13.35%, respectively) (Table 1; Fig. 1). In contrast, squid contained relatively low levels of 14:0, 16:1*n*–7, 18:2*n*–6, 18:4*n*–3, 20:1*n*–9, 20:4*n*–3, and 22:1*n*–11 and a low 22:1 isomer ratio in comparison with much higher levels of these components and ratios in mackerel (Table 1; Fig. 1).

Although average values of fatty acids differed between prey species, there was considerable intraspecific variability. For example, the levels of 18:2*n*–6 and 20:4*n*–3 in squid ranged between 0.19 and 1.00% (CV = 52.6%) and between 0.08 and 0.58% (CV = 66.2%), respectively, and in mackerel ranged between 0.81 and 1.87% (CV = 18.4%) and between 0.58 and 1.10% (CV = 15.7%), respectively. Similar variation was found in major fatty acids, such as 20:1*n*–9 (3.91–14.42% in mackerel and 3.04–8.46% in squid) and 22:6*n*–3 (8.35–17.96% in mackerel and 23.82–39.80% in squid).

Cod composition

During the first 6 weeks on the squid diet, the fat content of cod remained at 2.3%. However, during the following 8 weeks on the mackerel diet, the fat content of the whole cod increased to 3.7% ($P < 0.02$) (Table 1). The fatty acid composition of cod also changed significantly over the course of the experiment (MANOVA on cod treatments, $P < 0.0001$) (Table 1). Between-tank differences were found only when two minor fatty acids (iso16:0 and 16:3*n*–1) were included in the two-way analysis ($P < 0.0025$); with their removal, no tank differences were detected ($P > 0.1909$). Hence, data from all tanks were pooled for further analyses. After 3 weeks on the squid diet (CodS1), levels of 22:6*n*–3 significantly increased from those observed in baseline CodC, while 14:0, 16:1*n*–7, 18:2*n*–6, 18:4*n*–3, 20:1*n*–9, 20:1*n*–9, and 22:1*n*–11 significantly decreased ($P < 0.05$) (Fig. 1; Table 1). Fatty acid 20:5*n*–3 also increased and 20:4*n*–3 and the 22:1 ratio decreased; however, these changes were less pronounced, reflecting the relative similarity in levels of these components in the two diets (CodC and squid). After 6 weeks on the squid diet (CodS2), levels of fatty acids still differed from the baseline cod but there were no significant differences between CodS1 and CodS2 ($P > 0.1$).

After the first 5 weeks on the mackerel diet (CodM1), the levels of 14:0, 16:1*n*–7, 18:2*n*–6, 18:4*n*–3, 20:1*n*–9, 20:4*n*–3, and 22:1*n*–11 and the 22:1 ratio increased significantly ($P < 0.005$), while the levels of 20:4*n*–6, 20:5*n*–3, and 22:6*n*–3 decreased significantly ($P < 0.002$) from levels found at the end of the squid diet. These changes corresponded to the respective differences in these components found between mackerel and squid (Fig. 1; Table 1). The fatty acid signature of cod fed mackerel for 8 weeks (CodM2) again differed from the cod fed squid (CodS1 and CodS2) but did not differ further from CodM1 ($P > 0.1$). The percentage of one major fatty acid, 18:1*n*–9, did not decrease from CodC to CodS1 and CodS2 as might have been expected by low levels found in squid (Table 1). However, after the switch from squid (3.40% 18:1*n*–9) to mackerel (9.15% 18:1*n*–9), this component significantly increased as expected in CodM1 and CodM2 ($P < 0.01$). In general, the levels of most fatty acids changed between dietary treatments, but did not differ further within treatments, i.e., between CodM1 and CodM2 or between CodS1 and CodS2.

CART analysis was performed using all 74 fatty acids to determine which fatty acids best identified the differences among cod dietary treatments and to determine how well the dietary treatments could be correctly classified (Fig. 2). The CART algorithm selected a minor component, 16:3*n*–1, as the fatty acid that maximized the change in deviance (91.8) between groups at the root node. All 20 of the baseline cod (CodC) were correctly classified on the left-hand side of the tree and all cod in the dietary treatment groups, with the exception of five CodS1, were grouped on the right-hand side of the tree. Subsequent splits resulted in most of the cod fed squid (CodS1 and CodS2) being grouped closer to the baseline cod (CodC) and classified in center branches, while cod fed mackerel (CodM1 and CodM2) were grouped in the right-hand branches and separated from both baseline cod and cod fed squid (Fig. 2). This tree correctly classified 93% (97 of 104) of the cod based upon their fatty acid signatures; five of the seven individuals misclassified were the result of difficulty separating CodM1 from CodM2 and CodS1 from CodS2.

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Table 1. Fatty acid composition (mass %) of prey species (squid and Atlantic mackerel) and Atlantic cod after dietary treatments.

	Squid ($N = 18$)	Mackerel ($N = 25$)[a]	CodC ($N = 20$)	CodS1 ($N = 20$)	CodS2 ($N = 20$)	CodM1 ($N = 20$)	CodM2 ($N = 24$)
% lipid	2.0±0.21	15.8±0.61	2.3±0.23	1.8±0.21	2.3±0.22	3.7±0.26	3.6±0.31
Fatty acid							
12:0	0.02±0.00	0.05±0.00	0.02±0.00	0.00±0.00	0.00±0.00	0.01±0.00	0.02±0.00
13:0	0.00±0.00	0.26±0.03	0.00±0.00	0.00±0.00	0.00±0.00	0.27±0.09	0.00±0.00
iso14	0.06±0.01	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
14:0[b]	2.04±0.20	4.19±0.12	2.32±0.15	1.56±0.11	1.77±0.09	2.48±0.07	2.40±0.08
14:1*n*–9	0.06±0.01	0.29±0.02	0.13±0.01	0.10±0.00	0.11±0.01	0.22±0.00	0.21±0.00
14:1*n*–7	0.05±0.01	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
iso15	0.08±0.01	0.21±0.00	0.14±0.00	0.10±0.00	0.10±0.00	0.15±0.00	0.15±0.00
anti15	0.05±0.01	0.10±0.00	0.03±0.00	0.01±0.00	0.01±0.00	0.06±0.00	0.05±0.00
15:0	0.78±0.12	0.47±0.01	0.37±0.01	0.32±0.00	0.32±0.00	0.37±0.00	0.36±0.00
iso16[b]	0.29±0.04	0.17±0.00	0.09±0.00	0.21±0.02	0.22±0.00	0.16±0.00	0.15±0.01
16:0[b]	19.57±0.50	13.45±0.35	14.47±0.37	14.70±0.27	14.41±0.23	12.77±0.24	12.29±0.27
16:1*n*–11[b]	0.26±0.02	0.59±0.04	1.05±0.68	0.39±0.01	0.41±0.00	0.49±0.02	0.55±0.03
16:1*n*–9	0.09±0.01	0.24±0.01	0.34±0.00	0.40±0.01	0.38±0.00	0.33±0.00	0.37±0.00
16:1*n*–7[b]	1.30±0.27	5.48±0.33	4.47±0.28	3.36±0.28	3.64±0.21	4.94±0.18	5.10±0.22
7Me16:0	0.16±0.02	0.37±0.01	0.26±0.00	0.24±0.00	0.24±0.00	0.29±0.00	0.30±0.00
16:1*n*–5	0.27±0.02	0.38±0.01	0.31±0.01	0.34±0.02	0.38±0.00	0.32±0.01	0.29±0.02
16:2*n*–6	0.10±0.02	0.01±0.00	0.00±0.00	0.03±0.02	0.00±0.00	0.03±0.00	0.03±0.00
iso17	0.12±0.01	0.20±0.01	0.17±0.01	0.17±0.00	0.18±0.00	0.18±0.00	0.18±0.00
16:2*n*–4	0.29±0.03	0.46±0.03	0.47±0.06	0.53±0.03	0.58±0.02	0.56±0.02	0.56±0.02
16:3*n*–6	0.04±0.02	0.26±0.03	0.17±0.07	0.15±0.04	0.17±0.02	0.25±0.01	0.25±0.02
17:0	0.68±0.03	0.38±0.02	0.23±0.01	0.33±0.02	0.33±0.01	0.32±0.00	0.31±0.00
16:3*n*–4	0.12±0.02	0.15±0.03	0.24±0.01	0.13±0.02	0.11±0.02	0.16±0.00	0.17±0.01
17:1	0.16±0.02	0.44±0.03	0.39±0.01	0.39±0.02	0.34±0.02	0.38±0.00	0.40±0.01
16:3*n*–1[b]	0.34±0.08	0.31±0.02	0.05±0.00	0.22±0.03	0.26±0.01	0.22±0.01	0.24±0.01
16:4*n*–3	0.13±0.03	0.05±0.03	0.00±0.00	0.00±0.00	0.00±0.00	0.02±0.00	0.00±0.00
16:4*n*–1	0.35±0.03	0.33±0.03	0.38±0.02	0.51±0.03	0.46±0.04	0.15±0.01	0.18±0.03
iso18	0.17±0.02	0.02±0.00	0.38±0.04	0.46±0.05	0.36±0.03	0.21±0.02	0.21±0.03
anti18	0.11±0.02	0.00±0.00	0.28±0.04	0.12±0.05	0.05±0.02	0.20±0.02	0.18±0.02
18:0[b]	3.95±0.21	2.48±0.12	3.03±0.11	3.37±0.12	3.11±0.07	2.63±0.06	2.71±0.05
18:1*n*–13	0.11±0.02	0.11±0.02	0.00±0.00	0.08±0.02	0.03±0.01	0.03±0.01	0.00±0.00
18:1*n*–11	0.20±0.03	0.48±0.03	0.87±0.09	1.10±0.09	1.22±0.09	1.14±0.04	1.20±0.09
18:1*n*–9[b]	3.40±0.33	9.15±0.73	10.30±0.31	10.97±0.32	10.47±0.36	11.61±0.28	12.14±0.35
18:1*n*–7	1.42±0.12	3.13±0.12	4.15±0.65	4.03±0.47	3.87±0.59	4.10±0.62	4.20±0.40
18:1*n*–5	0.39±0.03	0.63±0.02	0.39±0.08	0.38±0.07	0.38±0.09	0.54±0.09	0.54±0.10
18:2d5,7	0.03±0.00	0.04±0.00	0.03±0.03	0.06±0.03	0.05±0.04	0.10±0.05	0.09±0.06
18:2*n*–7	0.06±0.01	0.01±0.00	0.08±0.04	0.02±0.03	0.00±0.00	0.00±0.00	0.00±0.00
18:2*n*–6[b]	0.44±0.06	1.47±0.05	0.95±0.16	0.85±0.18	0.84±0.14	1.20±0.12	1.24±0.17
18:2*n*–4	0.18±0.02	0.12±0.01	0.18±0.05	0.12±0.04	0.12±0.04	0.13±0.03	0.14±0.03
18:3*n*–6	0.08±0.00	0.12±0.00	0.05±0.03	0.08±0.03	0.08±0.01	0.10±0.01	0.10±0.01
18:3*n*–4	0.09±0.00	0.11±0.00	0.05±0.02	0.12±0.04	0.09±0.06	0.08±0.02	0.07±0.03
18:3*n*–3[b]	0.30±0.05	1.43±0.09	0.66±0.22	0.44±0.20	0.48±0.19	0.93±0.13	1.00±0.20
18:3*n*–1	0.05±0.00	0.02±0.00	0.06±0.03	0.10±0.02	0.11±0.02	0.12±0.04	0.12±0.05
18:4*n*–3[b]	0.36±0.09	2.73±0.12	1.04±0.49	0.75±0.43	0.82±0.41	1.72±0.30	1.82±0.53
18:4*n*–1	0.06±0.01	0.08±0.01	0.10±0.04	0.07±0.03	0.08±0.04	0.10±0.03	0.10±0.03
20:0	0.11±0.00	0.12±0.00	0.07±0.02	0.05±0.03	0.05±0.02	0.05±0.00	0.05±0.01
20:1*n*–11	0.60±0.04	0.73±0.03	0.58±0.23	0.56±0.20	0.61±0.19	0.72±0.11	0.69±0.12
20:1*n*–9[b]	4.81±0.41	8.01±0.53	4.64±1.83	3.49±1.15	4.05±1.35	5.35±1.05	5.51±1.01
Ratio 20:1	0.13±0.00	0.10±0.00	0.13±0.03	0.16±0.02	0.15±0.02	0.14±0.02	0.13±0.02
20:1*n*–7[b]	0.21±0.03	0.84±0.07	0.40±0.12	0.31±0.07	0.30±0.06	0.46±0.13	0.45±0.11
20:1*n*–5	0.05±0.00	0.11±0.00	0.09±0.05	0.09±0.03	0.08±0.02	0.10±0.02	0.09±0.01
20:2*n*–6	0.33±0.00	0.31±0.01	0.25±0.05	0.26±0.04	0.25±0.04	0.30±0.02	0.31±0.04
20:3*n*–6	0.02±0.00	0.05±0.00	0.05±0.01	0.06±0.02	0.05±0.01	0.06±0.00	0.07±0.01
20:4*n*–6	1.52±0.09	0.44±0.05	2.45±1.45	2.98±1.55	2.17±0.83	1.32±0.43	1.31±0.57
20:3*n*–3	0.75±0.09	0.19±0.01	0.11±0.03	0.12±0.03	0.13±0.04	0.18±0.04	0.19±0.04

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Table 1 (*concluded*).

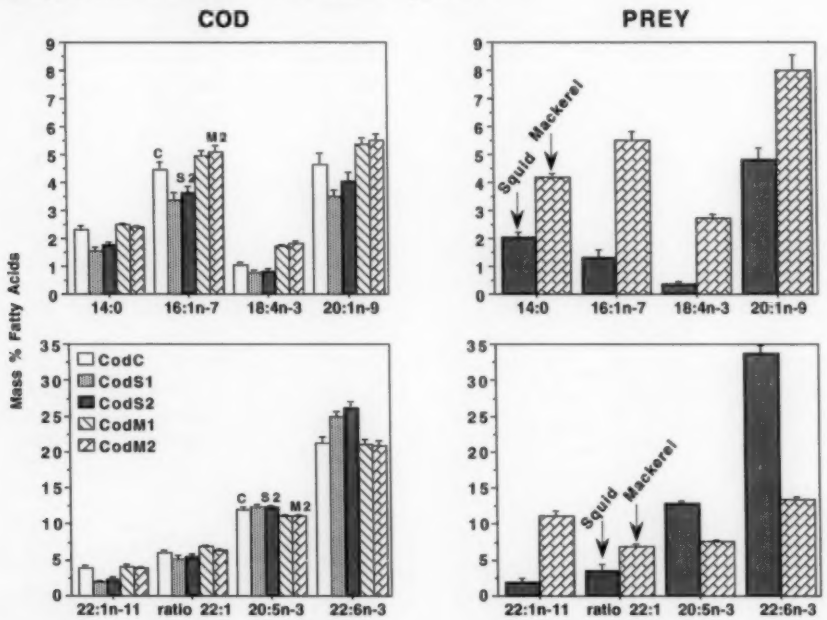
	Squid ($N = 18$)	Mackerel ($N = 25$)[a]	CodC ($N = 20$)	CodS1 ($N = 20$)	CodS2 ($N = 20$)	CodM1 ($N = 20$)	CodM2 ($N = 24$)
20:4*n*–3[b]	0.23±0.04	0.84±0.03	0.47±0.14	0.45±0.16	0.48±0.13	0.78±0.10	0.82±0.13
20:5*n*–3[b]	12.93±0.32	7.54±0.16	11.98±1.50	12.43±1.01	12.32±1.06	11.06±0.94	11.08±1.28
22:0	0.03±0.00	0.00±0.00	0.07±0.04	0.03±0.04	0.00±0.00	0.00±0.00	0.00±0.00
22:1*n*–11[b]	1.96±0.60	11.09±0.82	3.84±1.82	1.94±1.04	2.36±1.20	4.10±1.10	3.80±1.08
22:1*n*–9[b]	0.43±0.04	1.69±0.11	0.62±0.30	0.34±0.12	0.41±0.12	0.61±0.22	0.61±0.16
Ratio 22:1[b]	3.57±0.81	6.81±0.40	5.94±1.94	5.12±2.11	5.44±1.70	6.89±1.12	6.31±1.23
22:1*n*–7	0.09±0.00	0.28±0.03	0.10±0.03	0.11±0.03	0.08±0.02	0.09±0.03	0.07±0.04
22:1*n*–5	0.12±0.00	0.00±0.00	0.05±0.04	0.04±0.03	0.02±0.03	0.02±0.03	0.00±0.03
22:2*n*–6	0.02±0.00	0.03±0.00	0.00±0.01	0.03±0.03	0.01±0.02	0.03±0.01	0.02±0.02
21:5*n*–3	0.18±0.01	0.30±0.00	0.22±0.06	0.20±0.07	0.22±0.06	0.31±0.04	0.32±0.06
22:4*n*–6	0.11±0.00	0.06±0.00	0.19±0.12	0.18±0.11	0.15±0.07	0.11±0.04	0.12±0.05
22:5*n*–6	0.49±0.03	0.29±0.02	0.38±0.08	0.38±0.05	0.34±0.05	0.35±0.07	0.32±0.06
22:4*n*–3	0.04±0.00	0.08±0.00	0.04±0.03	0.04±0.02	0.05±0.02	0.06±0.01	0.09±0.08
22:5*n*–3	0.59±0.04	1.39±0.04	1.77±0.22	1.78±0.22	1.69±0.16	1.61±0.08	1.68±0.16
22:6*n*–3[b]	33.77±1.14	13.35±0.43	21.15±4.20	24.99±3.14	26.10±3.93	21.02±2.83	20.84±3.53
24:1	0.58±0.04	1.09±0.04	1.06±0.24	1.35±0.50	1.20±0.30	0.81±0.20	0.78±0.22

Note: Values are means ± SEM. CodC, baseline cod on cod diet, week 0; CodS1 and CodS2, cod on squid diet for 3 and 6 weeks, respectively; CodM1 and CodM2, cod on mackerel diet for 5 and 8 weeks, respectively.

[a]Mackerel as fed to cod, i.e., with heads, tails, and viscera removed.

[b]Fatty acids chosen ($N = 19$) to test treatment and tank differences using MANOVA, based upon abundance and (or) relevance to dietary differences.

Fig. 1. Relative amounts (% by mass) of selected abundant fatty acids in Atlantic cod dietary treatment groups and prey. Bars are means and vertical lines are 1 SEM for CodC (baseline cod fed cod), CodS1 and CodS2 (cod fed squid diet for 3 and 6 weeks, respectively), and CodM1 and CodM2 (cod then changed to a mackerel diet for 5 and 8 weeks, respectively).



As stated previously, the minor fatty acid 16:3*n*–1 was originally chosen at the first node of the tree (Fig. 2), as it produced the greatest deviance between groups. Choosing one of the more abundant fatty acids (e.g., 18:2*n*–6, 18:3*n*–3, 18:4*n*–3, 20:4*n*–3) with relatively high deviances (61.5–89.0) for the root node resulted in similar classifications of cod diet groups, but with higher misclassification rates (16–18 of 104).

Composition of cod dietary treatments in relation to prey composition

Although MANOVA showed that there were signifcant differences in the fatty acid composition of squid, mackerel, and wild cod, we used CART analysis to identify which fatty acids best identified these fish species and to determine how well the groups were classified. CART analysis accurately separated

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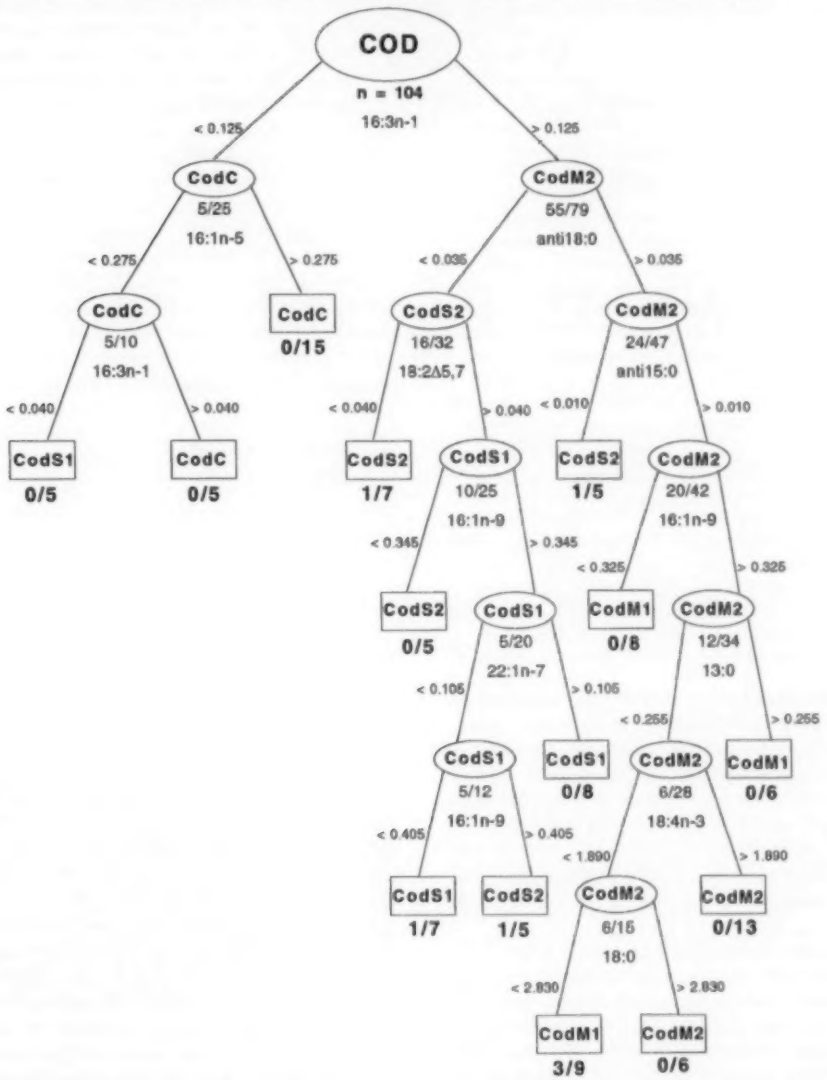
Fig. 2. Classification tree of all Atlantic cod dietary treatment groups. Elipses indicate intermediate splitting nodes and rectangles indicate terminal nodes where a classification is made. The labels within the ovals and rectangles indicate the classification of the group with the largest number of observations at that node. The fractions located beneath each split indicate the number of misclassifications over the total number of observations for that node. The fatty acids listed at each split, as well as their optimal splitting levels, were chosen by the algorithm to create that split (values < *X* down left extension, values > *X* down right extension). Total misclassification rate was 7/104. Rate of cod groups correctly classified was 93%: CodC (20/20), CodS1 (19/20), CodS2 (19/20), CodM1 (20/20), and CodM2 (19/24).



baseline cod, squid, and mackerel into their respective groups with no misclassifications (0 of 63) using only the two fatty acids 20:5*n*–3 and 16:1*n*–9.

Clearly, fatty acid patterns of cod changed in the direction of that found in their prey (Fig. 1). To examine whether cod could still be differentiated from squid and mackerel after having been fed pure squid and mackerel diets, CART analysis using all 74 fatty acids was performed on cod treatment groups and their diets (Fig. 3). To avoid an overly large and cumbersome tree, CodS1 and CodS2 were combined into one group and CodM1 and CodM2 were combined into another. Squid were clearly distinguished from the cod fed squid (CodS), while mackerel were readily distinguished from the cod fed mackerel (CodM). In this analysis, the cod dietary treatment groups continued to be distinguished from one another, although baseline cod and cod fed squid tended to group on the left-hand side of the tree with squid, while cod fed mackerel grouped on the right-hand side with mackerel (Fig. 3).

Discussion

To examine the influence of diet on the fatty acid signature of

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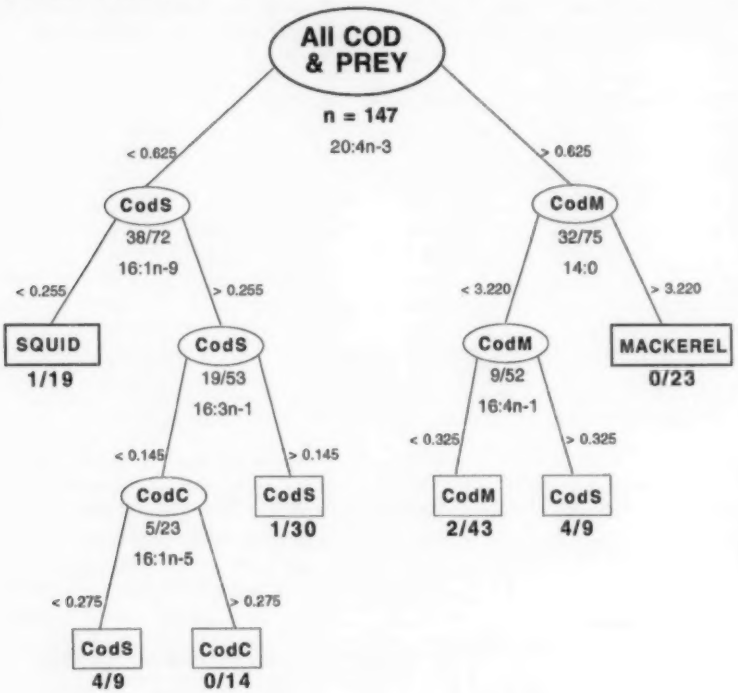
Fig. 3. Classification tree of prey and all Atlantic cod dietary treatment goups. See Fig. 2 for an explanation of the tree. For analysis, all cod on the squid diet (CodS1 and CodS2) were combined as CodS and all cod on the mackerel diet (CodM1 and CodM2) were combined as CodM. Total misclassification rate was 12/147. Rate of prey and cod groups correctly classified was 92%: squid (18/18), Atlantic mackerel (23/25), CodC (14/20), CodS (39/40), and CodM (41/44).



Atlantic cod, two natural prey items, which differ significantly in lipid content and fatty acid composition, were used in our study. Although adult wild cod feed on various prey items, including a wide variety of fish species as well as various invertebrates (Lilly 1991), we used these single-species diets to maximize the dietary effects on the cod fatty acid signature. Squid and mackerel were indeed quite different in their patterns of fatty acids (Fig. 1) and were easily differentiated from one another, even when only major fatty acids were considered.

Adult cod used in this study initially contained about 2.3% total body fat and did not change in fat content during the 6-week squid diet (containing 2.0% lipid) (Table 1). However, despite maintenance of total body fat, the composition of the fat changed significantly. After only 3 weeks of being fed a pure squid diet, the fatty acid patterns in cod changed in the direction of those as found in squid (Fig. 1). The magnitude of the changes in cod fatty acids also tended to reflect the relative magnitude in squid; for instance, levels of 20:5*n*–3 increased only slightly from baseline cod (CodC) to CodS1 and CodS2, while levels of 22:6*n*–3 increased more dramatically, reflecting the level of differences in these components between CodC and squid (Fig. 1). Additionally, despite being on a low-fat diet, the time course required for diet to influence total body lipids in cod appeared to be short. In only 3 weeks, cod fatty acid patterns were significantly altered in the direction expected by patterns in squid and did not differ further by 6 weeks.

After a second change in diet, cod again responded rapidly to changes in lipid intake. As expected on a high-fat diet (mackerel, 15.7%), adult cod deposited more total body fat than on a lower fat diet of either cod or squid (Table 1). As in the previous case with a switch to the squid diet, cod fatty acid patterns changed significantly to reflect the mackerel diet (Fig. 1). Most of the changes that had occurred on a diet of squid were reversed and further changed with a change to a diet of mackerel, and the changes reflected the direction of differences in the fatty acid compositions of the squid and mackerel diets. The finding that 18:1*n*–9 remained high in cod fed squid, despite a reduction in diet, suggests its synthesis in cod; however, it did increase as expected with its increase in the mackerel diet (Table 1). Initially, we did not expect that cod fatty acid signatures would change as rapidly as found in our study; thus, when cod reduced their food intake during the mackerel diet, they were not sampled until 5 and 8 weeks to ensure that any dietary effects could be measured. But again, the time course required for diet to influence body lipids was relatively short. Cod fatty acid patterns changed significantly by 5 weeks and did not differ further at 8 weeks. It is not not known whether cod fatty acid patterns would have continued to change further with a longer time on each of the test diets. However, it would appear from our results that most changes had taken place within the first 3–5 weeks and subsequent changes over the next few weeks were not detectable.

Clearly, when switched first to a squid diet and then to a mackerel diet, the fatty acid signature of cod changed

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significantly toward the fatty acid signatures of these respective prey, thus demonstrating the value of fatty acid signatures in predators as indicators of diet. However, when applied to higher trophic level predators such as seals (Iverson 1993; Iverson et al. 1997*a*, 1997*b*), then the cod, as well as squid and mackerel, become potential prey. In the present study, fatty acid patterns in squid differed greatly from those of mackerel, and both were also readily distinguished from the original wild or baseline cod (CodC) using either MANOVA or CART. These findings suggest that fatty acid patterns in higher trophic level predators might be used to distinguish species compositions of diets. However, an additional question that arises is, if a predatory fish (i.e., cod) feeds upon another prey item and begins in part to resemble its prey item in fatty acid patterns, and both cod and prey are consumed by a larger predator, can the predatory fish and its prey items still be distinguished from one another. Our results indicate that the answer to this question is yes. The cod treatment groups were readily differentiated from one another using both univariate and multivariate analyses (e.g., Fig. 2). However, despite the significant changes in cod fatty acid signatures, cod were still readily separated from their dietary items using CART analysis (Fig. 3). In Alaska, Iverson et al. (1997*b*) also found that despite large within-species variation in fatty acid signatures with geographical region and likely diet, fish species were still readily differentiated from one another. Additionally, even though walleye pollock (*Theragra chalcogramma*) and Pacific herring (*Clupea pallasi*) of similar size-classes in similar locations were known to have similar diets, they were still distinguished by species based upon their fatty acid signatures.

The species-specific differences in the fatty acid signatures of cod, squid, and mackerel provide support for the use of fatty acid signatures to investigate the diet of higher trophic level predators such as marine mammals (e.g., Iverson et al. 1997*b*). However, the changes within cod also point to the possibility of using fatty acids to study the foraging ecology of cod. We conclude that fatty acid signatures should allow useful analyses of trophic interactions and predator–prey relationships in both space and time. Our study shows that the deposition of dietary fatty acids accounts for a large part of the variation in Atlantic cod signatures and, as a result, suggests their use as an indicator of dietary intake. A feature, not to be overlooked, is that the characteristic fatty acid signatures appear to be integrated over a time course of weeks, offering the opportunity to extend our knowledge of fish diets obtained from research trawl surveys beyond that possible from stomach content data alone.

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References

Ackman, R.G., and Eaton, C.A. 1966. Lipids in the fin whale (*Balaenoptera physalus*) from North Atlantic waters. III. Occurrence of eicosenoic and docosenoic fatty acids in the zooplankton *Meganyctiphanes norvegica* (M. Sars) and their effect on whale oil composition. Can. J. Biochem. **44**: 1561–1566.

Bligh, E.G., and Dyer, W.J. 1959. A rapid method of total lipid extraction and purification. Can. J. Biochem. Physiol. **37**: 911–917.

Bowen, W.D., and Harrison, G.D. 1994. Offshore diet of grey seals *Halichoerus grypus* near Sable Island, Canada. Mar. Ecol. Prog. Ser. **112**: 1–11.

Bradstreet, R.B. 1965. The Kjeldahl method for organic nitrogen. Academic Press, New York.

Clarke, L.A., and Pregibon, D. 1992. Tree-based models. *In* Statistical models in S. *Edited by* J. M. Chambers and T.J. Hastie. Wadsworth and Brooks/Cole Advanced Books and Software, Chapman and Hall, New York. pp. 377–419.

Cowey, C.B., and Sargent, J.R. 1972. Fish nutrition. *In* Advances in marine biology. Vol. 10. *Edited by* Sir F. Yonge and Sir M. Yonge. Academic Press, London, U.K. pp. 383–492.

Dos Santos, J., Burkow, I.C., and Jobling, M. 1993. Patterns of growth and lipid deposition in cod (*Gadus morhua* L.) fed natural prey and fish-based feeds. Aquaculture, **110**: 173–189.

Iverson, S.J. 1988. Composition, intake and gastric digestion of milk lipids in pinnipeds. Ph.D. thesis. University of Maryland, College Park, Md.

Iverson, S.J. 1993. Milk secretion in marine mammals in relation to foraging: can milk fatty acids predict diet? Symp. Zool. Soc. Lond. **66**: 263–291.

Iverson, S.J., Sampugna, J., and Oftedal, O.T. 1992. Positional specificity of gastric hydrolysis of long-chain *n*–3 polyunsaturated fatty acids of seal milk triglycerides. Lipids, **27**: 870–878.

Iverson, S.J., Arnould, J.P.Y., and Boyd, I.L. 1997*a*. Milk fatty acid signatures indicate both major and minor shifts in the foraging ecology of lactating Antarctic fur seals. Can. J. Zool. **75**: 188–197.

Iverson, S.J., Frost, K.J., and Lowry, L.L. 1997*b*. Fatty acid signatures reveal fine structure of foraging distribution of harbor seals and their prey in Prince William Sound, Alaska. Mar. Ecol. Prog. Ser. **151**: 225–271

Kharlamenko, V.I., Zhukova, N.V., Khotimchenko, S.V., Svetachev, V.I., and Kamenev, G.M. 1995. Fatty acids as markers of food sources in a shallow-water hydrothermal ecosystem (Kraternaya Bight, Yankich Island, Kurile Islands). Mar. Ecol. Prog. Ser. **120**: 231–241.

Klungsøyr, J., Tilseth, S., Wilhelmsen, S., Falk-Petersen, S., and Sargent, J.R. 1989. Fatty acid composition as an indicator of food intake in cod larvae *Gadus morhua* from Lofoten, Northern Norway. Mar. Biol. **102**: 183–188.

Lee, R.F., Nevenzel, J.C., and Paffenhoffer, G.-A. 1971. Importance of wax esters and other lipids in the marine food chain: phytoplankton and copepods. Mar. Biol. **9**: 99–108.

Lie, O., Lied, E., and Lambertsen, G. 1986. Liver retention of fat and of fatty acids in cod (*Gadus morhua*) fed different oils. Aquaculture, **56**: 187–196.

Lilly, G.R. 1991. Interannual variability in predation by cod (*Gadus morhua*) on capelin (*Mallotus villosus*) and other prey off southern Labrador and northeastern Newfoundland. ICES Mar. Sci. Symp. **193**: 133–146.

Nelson, G.J. 1992. Dietary fatty acids and lipid metabolism. *In* Fatty acids in foods and their health implications. *Edited by* C.K. Chow. Marcel Dekker, New York. Chap. 19.

Sargent, J.R. 1989. The lipids. *In* Fish nutrition. *Edited by* J.E. Halver. Academic Press, Washington, D.C. Chap. 4.

Sargent, J.R., Parkes, R.J., Mueller-Harvey, I., and Henderson, R.J. 1988. Lipid biomarkers in marine ecology. *In* Microbes in the sea. *Edited by* M.A. Sleigh. Ellis Horwood Ltd., Chichester, U.K. pp. 119–138.

Smith, R.J., Hobson, K.A., Koopman, H.N., and Lavigne, D.M. 1996. Distinguishing between populations of fresh- and salt-water

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harbour seals (*Phoca vitulina*) using stable-isotope ratios and fatty acid profiles. Can. J. Fish. Aquat. Sci. **53**: 272–279.

Smith, S.J., Iverson, S.J., and Bowen, W.D. 1997. Analysis of fatty acid signatures using classification trees: a new tool for investigating the foraging ecology of seals. Can. J. Fish. Aquat. Sci. **54**: 1377–1386.

St. John, M.A., and Lund, T. 1996. Lipid biomarkers: linking the utilization of frontal plankton biomass to enhanced condition of juvenile North Sea cod. Mar. Ecol. Prog. Ser. **131**: 75–85.

Venables, W., and Ripley, B. 1994. Modern applied statistics with S-Plus. Springer-Verlag, Heidleberg.

Xu, R., Hung, S.S.O., and German, J.B. 1993. White sturgeon tissue fatty acid compositions are affected by dietary lipids. J. Nutr. **123**: 1685–1692.

Yu, T.C., Sinnhuber, R.O., and Putnam, G.B. 1977. Effect of dietary lipids on fatty acid composition of body lipid in rainbow trout (*Salmo gairdneri*). Lipids, **12**: 495–499.

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Incubation temperature, developmental biology, and the divergence of sockeye salmon (*Oncorhynchus nerka*) within Lake Washington

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Abstract: Sockeye salmon (*Oncorhynchus nerka*) introduced into Lake Washington in the 1930s and 1940s now spawn at several different sites and over a period of more than 3 months. To test for evolutionary divergence within this derived lineage, embryos that would have incubated in different habitats (Cedar River or Pleasure Point Beach) or at different times (October, November, or December in the Cedar River) were reared in the laboratory at 5, 9, and 12.5°C. Some developmental variation mirrored predictions of adaptive divergence: *(i)* survival at 12.5°C was highest for embryos most likely to experience such temperatures in the wild (Early Cedar), (*ii*) development rate was fastest for progeny of late spawners (Late Cedar), and (*iii*) yolk conversion efficiency was matched to natural incubation temperatures. These patterns likely had a genetic basis because they were observed in a common environment and could not be attributed to differences in egg size. The absolute magnitude of divergence in development rates was moderate (Late Cedar embryos emerged only 6 days earlier at 9°C) and some predictions regarding development rates were not supported. Nonetheless our results provide evidence of adaptive divergence in only 9–14 generations.

Résumé : Le saumon rouge (*Oncorhynchus nerka*) introduit dans le lac Washington dans les années 30 et 40 fraye maintenant à plusieurs endroits différents et sur une période de plus de 3 mois. Pour établir s'il y a eu divergence évolutionnaire chez cette lignée dérivée, des embryons qui auraient été incubés dans des habitats différents (rivière Cedar ou plage Pleasure Point) et à des périodes différentes (octobre, novembre ou décembre dans la rivière Cedar) ont été élevés en laboratoire à 5, 9 et 12,5°C. Certaines variations dans le développement correspondaient aux prédictions de divergence adaptative, notamment : *(i)* la survie à 12,5°C était plus élevée chez les embryons les plus susceptibles d'être exposés à une telle température dans le milieu d'origine (ponte hâtive, rivière Cedar), (*ii*) le taux de développement était plus élevé chez la progéniture des géniteurs tardifs (ponte tardive, rivière Cedar) et (*iii*) l'efficacité de conversion du vitellus concordait avec les températures d'incubation dans le milieu. Ces tendances sont probablement d'origine génétique parce qu'elles ont été observées dans un environnement commun et ne pouvaient être attribuées à des différences dans la taille des oeufs. L'ampleur absolue de la divergence au plan des taux de développement était modérée (les embryons tardifs de la rivière Cedar ne sont sortis de l'oeuf que 6 jours plus tôt à 9°C) et certaines prédictions concernant le taux de développement n'ont pas été confirmées. Néanmoins nos résultats fournissent l'évidence de la divergence adaptive dans seulement les neuf à quatorze générations.
[Traduit par la Rédaction]

Introduction

Studies of introduced populations have yielded important insights into evolution, particularly in regard to rates and mechanisms of population divergence (Stearns 1983; Reznick et al. 1990; Svensson 1997; Hendry and Kinnison 1998). Pacific salmon (*Oncorhynchus* spp.) provide opportunities to study incipient population divergence because they have been successfully introduced into new locations, such as New Zealand, the Great Lakes, and Lake Washington. Studies within these systems have shown that salmon introductions can give rise to a suite of new breeding groups, some of which become reproductively isolated from the others (Gharrett and Thomason 1987; Hendry et al. 1996; Quinn et al. 1996). These new populations are often exposed to different habitats and have diverged phenotypically in adult life history and morphology following colonization (Hendry and Quinn 1997; Kinnison et al. 1998). What remains ambiguous, however, is the extent to which such divergence is genetically based, as opposed to environmental effects expressed through phenotypic plasticity.

The present study tests for genetic divergence in the developmental biology of Lake Washington sockeye salmon (*Oncorhynchus nerka*). From 1937 to 1945, hatchery-produced sockeye salmon were transferred from Baker Lake (Fig. 1) to Lake Washington (reviewed in Hendry 1995). The largest population established by these introductions was in the principal tributary to the lake, the Cedar River. Then, in 1957, sockeye salmon were first observed spawning at certain beaches along the shores of Lake Washington (Woodey 1966). The largest of these beach-spawning aggregations was at

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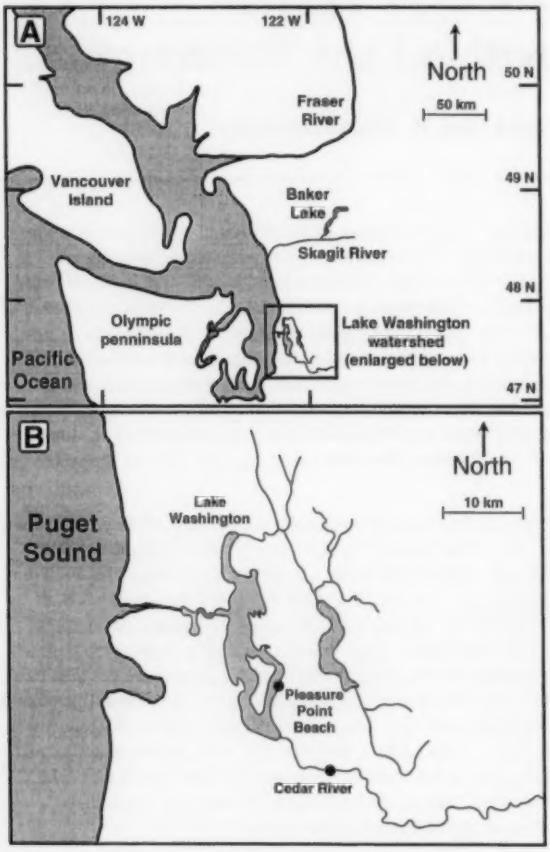
Fig. 1. Locations of (A) Lake Washington and Baker Lake and (B) the Cedar River and Pleasure Point Beach. Solid circles indicate collection locations.



Pleasure Point, a site about 7 km north of the Cedar River. Allelic variation at allozyme and microsatellite loci has revealed that the Pleasure Point population is also of the Baker Lake lineage and was most likely colonized by straying from the Cedar River (Hendry et al. 1996; J.K. Wenburg and A.P. Hendry, unpublished data). Since the founding event, however, Pleasure Point spawners have become at least partially reproductively isolated from Cedar River spawners (J.K. Wenburg and A.P. Hendry, unpublished data), enhancing the potential for their adaptive divergence.

River and beach spawning areas differ markedly in environmental features that influence salmonid evolution (Blair et al. 1993; Wood 1995; Taylor et al. 1997). Adult salmon spawning in the Cedar River experience strong currents and their embryos are exposed to frequent scouring events (Thorne and Ames 1987). In contrast, adults at Pleasure Point spawn in the near absence of current and their embryos incubate in stable substrates (Woodey 1966). These dramatic habitat differences suggest that selection should contribute to adaptive divergence of the two populations. In a pattern consistent with beach–river divergence in other lake systems, Cedar River females were longer than Pleasure Point females, and Pleasure Point males were deeper bodied (for their length) than Cedar River males (Hendry and Quinn 1997). These findings implied adaptive divergence owing to some combination of plasticity and genetic change since the beach site was colonized.

Examining variation in developmental characteristics under controlled conditions allows a test for divergence that is not confounded by phenotypic plasticity. Such a comparison within Lake Washington should prove informative because beach and stream incubation environments often differ in incubation temperature, which can lead to adaptive differentiation (Brannon 1987). For Lake Washington, we predicted that, in comparisons at a common temperature, embryos from populations that naturally incubate in warm water should take longer to develop than those from populations that naturally incubate in colder water. Such divergence would reduce hatching and emergence asynchrony caused by the otherwise positive correlation between incubation temperature and development rate (Brannon 1987). We also predicted that yolk conversion should be most efficient at laboratory temperatures approximating those that embryos would have experienced in the wild (Beacham and Murray 1987, 1989).

Selective regimes can also differ among fish that spawn or incubate at different times, even if they do so at the same location (e.g., Taylor 1980). Accordingly, some rivers accommodate seasonally distinct conspecific populations (Gharrett and Smoker 1993; Tallman and Healey 1994) that have adapted to their specific incubation conditions (Tallman 1986; Tallman and Healey 1991). Although the Cedar River does not contain discrete seasonal runs, the spawning period stretches from early October through early January. Because the tendency to spawn at a particular time is inherited (Gharrett and Smoker 1993), the extent of gene flow within populations such as the Cedar River should be negatively correlated with the spread in spawning time (isolation-by-time).

Thus, the embryos of fish that spawn at different times should be able to adapt, at least in part, to their specific thermal regimes (adaptation-by-time). For the Cedar River, we predicted that embryos likely to experience high temperatures in the wild should be those demonstrating the best survival at such temperatures in the laboratory. We also predicted that embryos beginning incubation late should take less time to develop than those beginning incubation early, when compared at a common temperature (Brannon 1987; Tallman and Healey 1991). We tested our predictions by incubating the embryos of spawning sockeye salmon that were collected at different times or places within Lake Washington at each of three different temperatures.

Methods

Study sites, temperature regimes, and gamete collection

The Cedar River is the largest tributary to the Lake Washington watershed and anadromous salmonids spawn in its lower 34.8 km. Most spawning takes place from late September through late December, with the peak in late October, and the annual number of spawners from 1967 to 1991 ranged between 76 000 and 350 000 (R. Egan, Washington Department of Fish and Wildlife, Mail Stop 43151, 600 Capitol Way N., Olympia, Wash., unpublished data). Cedar River water temperatures were obtained for October 1 – May 16 for each of the last 16 years (1980–1995) from the U.S. Geological Survey (1201 Pacific Avenue, Suite 520, Tacoma, Wash.). These data had been recorded at a gauging station 2.7 km upstream from the river mouth. At Cavanaugh Pond (a side channel–pond beside the Cedar

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Table 1. Incubation temperatures in the laboratory and in the wild, and the predicted and observed days spent in each developmental stage at each laboratory temperature.

	Fertilization to hatching				Hatching to emergence			
	Early Cedar	Middle Cedar	Late Cedar	Pleasure Point	Early Cedar	Middle Cedar	Late Cedar	Pleasure Point
Laboratory, 5°C								
Mean temperature	5.0	5.0	5.0	4.9	5.0	5.2	6.0	5.2
Predicted days	123	123	123	123	66	64	—	64
Observed days	123	124	120	124	60	55	—	53
Laboratory, 9°C								
Mean temperature	9.0	8.9	8.8	8.9	8.7	8.6	9.1	8.5
Predicted days	77	78	78	78	45	45	44	45
Observed days	76	77	74	76	40	39	36	38
Laboratory, 12.5°C								
Mean temperature	12.2	12.2	12.4	12.2	12.3	12.6	12.3	12.6
Predicted days	57	57	56	57	31	30	—	30
Observed days	54	54	51	53	24	25	—	26
Wild								
Mean temperature	6.8	6.0	6.4	9.9	6.5	8.6	9.9	9.9
Min. temperature	1.5	1.0	1.0	9.8	1.0	5.5	6.5	9.8
Max. temperature	12.0	9.5	11.5	9.9	10.0	13.0	15.5	9.9

Note: Predicted number of days in each period at each temperature were calculated using the Salmonid Incubation Program (Jensen 1988). Predicted days from hatching to emergence were invariably longer than those observed because Jensen's (1988) model uses maximum alevin wet weight, which typically occurs slightly after emergence. Degree-days can be calculated simply by multiplying the days in a given time period by the average temperature over that period.

River at river km 10.3), a HOBO temperature logger (Onset Computer Corp., Pocasset, Mass.) was buried 30 cm in the gravel in the center of the main spawning area (January 8 – March 27, 1996).

The Pleasure Point Beach lies about 7 km north of the Cedar River (Fig. 1) and has about 700 m^2 of spawning area (A.P. Hendry, unpublished data). Annual escapements at Pleasure Point have been estimated at 100–1000 (1963–1965, Woodey 1966) and 520–8180 (1976–1991, R. Egan, unpublished data). Estimates for the more recent of these two periods include several other beach sites near Pleasure Point, but spawners at these other sites are much less abundant. Spawning at Pleasure Point typically takes place between early November and early January, with the peak in late November (R. Egan, unpublished data), and the embryos incubate in upwelling groundwater (Woodey 1966). To record incubation temperatures at Pleasure Point, two HOBOs were buried 30 cm below the surface of the gravel, 5 m away from each other and near the center of the spawning area (November 1, 1995 – March 28, 1996).

Cedar River sockeye salmon were collected from a weir at river km 10.4 (as part of a hatchery program that began in 1991, Seiler and Kishimoto 1996). We obtained gametes from adults collected at this weir in 1995 and spawned on either October 21 (Early Cedar) or November 20 (Middle Cedar). The weir was removed in early December and the river remained very high and turbid throughout that month. Therefore, our final Cedar River collection (December 21, Late Cedar) was made using landing nets in Cavanaugh Pond, which joins the river about 100 m downstream from the weir. Cavanaugh Pond embryos incubate in Cedar River water that seeps through a berm separating the pond from the main river. At Pleasure Point, spawning fish were collected using a beach seine on November 18 (1995), gametes were squeezed gently from six males and six females, and all fish were then released. The number of females in each collection (six) was chosen to minimize potential impacts on the small Pleasure Point population.

Laboratory rearing

Gametes were transported in coolers to the laboratory within 2 h of their collection. For each female, a sample of about 50 eggs was blotted dry, weighed, and counted to determine average egg weight. The remaining eggs for each female were then fertilized (each by a separate male), giving rise to six full-sib families for each of the four collections. Three Heath stacks were plumbed so that one received 12.5°C water, one 9°C water, and one 5°C water (Table 1). Water flowed through the stacks at a rate of 11.4 $L \cdot min^{-1}$ and each incubation tray held six PVC egg cups (internal diameter = 8 cm). Eggs from each of the 24 experimental families were divided into six lots of 100, and these lots were randomly assigned to egg cups (two separate egg cups for each family at each of the three temperatures). The stacks were draped with black plastic to eliminate light.

At 55, 33, and 30 days postfertilization (at 5, 9, and 12.5°C, respectively), all dead eggs were counted and removed from each egg cup. Eggs were checked periodically thereafter and mortalities removed and counted. Survival from fertilization to hatching (percent) was calculated for each family at each temperature as the mean of its survival in the two egg cups. After hatching commenced, the numbers of live and dead eggs and alevins in each cup were counted daily. The mean and median dates of hatching were calculated for each cup and then averaged for the two cups from each family, at each temperature.

On the first day that at least 95% of the embryos had hatched within a family, 100 of them (randomly chosen from the two egg cups) were transferred to PVC emergence chambers maintained at the same temperature that each family had experienced prior to hatching (Table 1). Alevins incubated in a substrate of glass marbles and, at emergence, swam upward through 16 cm of water, exiting the chamber through a notch at the top and falling a short distance into a surrounding tub (see Hendry 1995 for details on the emergence chambers). Emergence chambers were shielded with a translucent cover that permitted diffuse light on a natural photoperiod to reach the upper layer of the marble substrate. The tubs surrounding each emergence chamber were checked daily for newly emerged fry, which were removed, counted, killed with an overdose of MS 222, and preserved in 10% buffered formalin. The mean and median dates of emergence were calculated for each family.

After about 100 days of preservation, every 10th fry to have emerged was measured (fork length to the nearest 0.1 mm) and weighed (wet weight to the nearest milligram), and the yolk was removed and weighed (wet weight to the nearest milligram). Family

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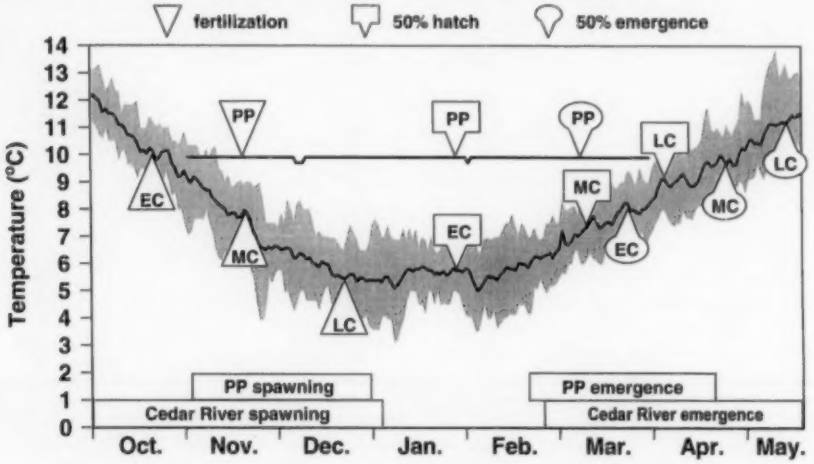
Fig. 2. Temperature profiles for Pleasure Point (upper line) and the Cedar River (lower line and shaded area); fertilization dates for the Early Cedar (EC), Middle Cedar (MC), Late Cedar (LC), and Pleasure Point (PP) collections; hatching and emergence dates for the embryos of each collection if they had incubated in the wild (predicted using Jensen's 1988 model); and periods of natural spawning and emergence (boxes along the *x*-axis). Temperature records for the Cedar River depict the 16-year average (line), the 10th percentile (lower boundary of the shaded area), and the 90th percentile (upper boundary of the shaded area). Natural spawning times are from stream surveys (R. Egan, unpublished data), emergence times for the Cedar River are the period during which 90% of the fry emigrate to the lake (Seiler and Kishimoto 1996), and emergence times for Pleasure Point were estimated from spawning times and natural incubation temperatures.



means were calculated for fry length, fry weight (with yolk), tissue weight (without yolk), and proportion yolk (percent) at each temperature.

Statistical analysis

Median values for days to hatching and emergence were not analyzed further because they were nearly identical to the mean values. All statistical analyses were based on family means (the mean value for the offspring of each full-sib mating) at each temperature because this was the appropriate unit of replication for comparing the development of embryos from the four collections. The effects of temperature, collection, and their interaction were analyzed using split-plot ANOVA models (SPSS version 7.5) because each full-sib family had been divided among three temperatures. Egg size varied among the four collections (see Results), so it was added as a covariate to the ANOVA models. When an effect of egg weight was detected, the trait was compared among groups at a common egg weight (i.e., comparison of adjusted means, Huitema 1980). Tukey tests were used for post hoc pairwise comparisons among collections within temperatures, when such interpretations were necessary to evaluate our predictions.

Late Cedar fry were excluded from the split-plot ANOVAs associated with emergence (days to emergence, fry length, fry weight, tissue weight, and proportion yolk) because they experienced higher temperatures after hatching (in the cold treatment) and because many escaped from the chambers during an overflow (in the warm treatment). However, one-way ANOVAs and Tukey tests were used to compare fry among all four collections at 9°C, where such problems did not occur. One Middle Cedar family experienced 100% mortality at all temperatures and was excluded from the analyses. Hypothesis testing was conducted at $\alpha = 0.05$, but interactions were considered significant at $P < 0.10$ (a conservative approach to the interpretation of main effects).

Results

Natural temperature regimes

Cedar River temperatures (monitored over the past 15 years) decreased through the spawning season and increased through the hatching and emergence period (Fig. 2). No information is available on spatial variation in Cedar River temperatures, but there are no major tributaries and the vast majority of spawning takes place in the lower main stem of the river. During the incubation period, average daily temperature did not differ between the Cavanaugh Pond collection site and the Cedar River gauging station (average difference = 0.09°C, paired *t*-test, two-tailed $P = 0.40$). At Pleasure Point, temperatures were effectively isothermal (9.8–9.9°C), and nearly identical thermal regimes were recorded by the two different temperature loggers. Embryos from the different collections would have experienced dramatically different temperature regimes if they had incubated in the wild (Fig. 2).

Developmental biology

Average egg weight differed slightly among the four collections (one-way ANOVA, $P = 0.03$). When added as a covariate to the ANOVA models, egg weight did not significantly influence survival to hatching ($P = 0.07$), days to hatching ($P = 0.12$), days to emergence ($P = 0.10$), or proportion yolk at emergence ($P = 0.51$). In contrast, fry length, fry weight, and tissue weight at emergence were positively correlated with egg weight ($P < 0.001$, $P = 0.01$, and $P = 0.007$, respectively).

Split-plot ANOVAs indicated that survival to hatching (arcsine transformed) was considerably higher at 5 and 9°C than at 12.5°C ($P < 0.001$; Fig. 3) but that survival did not differ consistently among the four collections ($P = 0.38$). There was, however, a significant interaction between temperature and collection ($P < 0.001$) because Early Cedar embryos had higher survival than Middle Cedar embryos ($P = 0.01$) and Pleasure Point embryos ($P = 0.02$) at 12.5°C (Fig. 3).

Days from fertilization to hatching were negatively correlated with water temperature ($P < 0.001$) but did not differ consistently among the four collections ($P = 0.10$) and there

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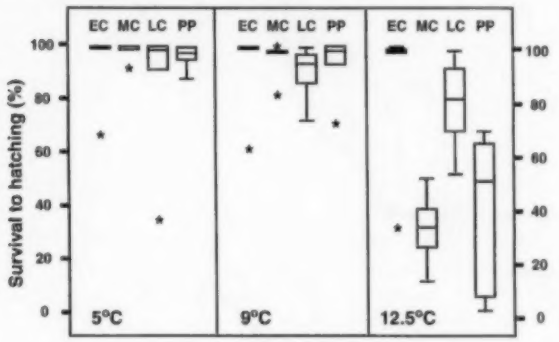
Fig. 3. Survival from fertilization to hatching at the three incubation temperatures for embryos from the Early Cedar (EC), Middle Cedar (MC), Late Cedar (LC), and Pleasure Point (PP) collections. The data are shown as the median, quartiles, and extreme values (asterisks) for family means.



was no interaction effect ($P = 0.22$). Within each temperature, Late Cedar embryos tended to hatch slightly earlier (Fig. 4A), but the only significant difference was at 12.5°C, where they hatched 3 days earlier than Early Cedar embryos ($P = 0.043$).

Days from fertilization to emergence were negatively correlated with water temperature ($P < 0.001$; Fig. 4B) but did not differ consistently among the Early Cedar, Middle Cedar, and Pleasure Point collections ($P = 0.12$). There was no interaction between temperature and collection ($P = 0.11$). At 9°C, Late Cedar alevins emerged 4–6 fewer days after fertilization than alevins from the other collections (one-way ANOVA, $P < 0.001$; $P < 0.008$ for each pairwise Tukey comparison). Although we excluded Late Cedar fry at 12.5 and 5°C from the emergence analysis (see Methods), qualitative observations indicated that they also emerged early at these temperatures, relative to other collections.

Fry length varied with incubation temperature ($P < 0.001$) and among the Early Cedar, Middle Cedar, and Pleasure Point collections ($P = 0.02$), but there was a strong interaction between temperature and collection ($P = 0.007$). This interaction arose because Pleasure Point fry were their longest at 9°C whereas fry from the other collections were their longest at 5°C (Fig. 5A). At 9°C (including the Late Cedar), Early Cedar fry were longest, Late Cedar and Middle Cedar fry were shortest, and Pleasure Point fry were intermediate in length ($P = 0.003$). If egg weight was included in the models, fry length did not differ among the collections ($P = 0.13$), except at 9°C, where Pleasure Point fry were largest at a standard egg weight ($P = 0.01$).

Fry emerging at 12.5°C weighed less (including yolk) than those at either 5 or 9°C ($P < 0.001$; Fig. 5B) and this trend was consistent for the different collections (no interaction, $P = 0.51$). Considering all three temperatures, fry weight did not differ consistently among the Early Cedar, Middle Cedar, and Pleasure Point collections ($P = 0.06$). At 9°C, however, Early Cedar fry were heavier than Late Cedar and Middle Cedar fry, and Pleasure Point fry were intermediate in weight ($P = 0.003$). When egg weight was included as a covariate, the collections no longer differed in fry weight ($P = 0.70$). The same trends were evident when tissue weight was used in the models instead of overall fry weight.

Proportion yolk at emergence (arcsine transformed) did not differ between 5 and 9°C but was greater overall at 12.5°C ($P < 0.001$). Proportion yolk differed among Early Cedar, Middle Cedar, and Pleasure Point fry ($P = 0.03$), but this difference varied somewhat with temperature (interaction, $P = 0.06$; Fig. 5C). At 9°C (including the Late Cedar), no differences were detected among the collections ($P = 0.08$).

Discussion

We investigated population divergence on a short time scale by quantifying developmental variation for introduced sockeye salmon that now incubate at different times or places within the Lake Washington watershed. Observed divergence was *(i)* consistent with our predictions based on incubation temperature, *(ii)* documented in a common laboratory environment at three different temperatures (reducing the likelihood that genetic effects were confounded by phenotypic plasticity), and *(iii)* not strongly influenced by differences in egg size (the most obvious maternal effect). We conclude that certain developmental features of sockeye salmon embryos can evolve in an apparently adaptive fashion in less than 9–14 generations (since 1957, when fish were first observed at Pleasure Point, or since 1937, when the introductions into Lake Washington began).

Temporal patterns of divergence

Cedar River fish that spawn in either mid-October, mid-November, or mid-December experience very different incubation conditions (Fig. 2). Genetic exchange would be limited among the fish that spawn at these different times because nuances of spawning behavior limit mixing within a breeding season (Hendry et al. 1995), and the high heritability of spawning date maintains much of the isolation across generations (Gharrett and Smoker 1993). Predictions for how developmental divergence might occur within the Cedar River population with respect to spawning date (and therefore, incubation time) were supported to varying degrees.

Survival from fertilization to hatching was high for most of the experimental families at both 5 and 9°C, but declined precipitously at 12.5°C for embryos from all collections except Early Cedar (Fig. 3). This pattern was consistent with the prediction that embryos from populations likely to experience high temperatures prior to hatching in the wild (see Early Cedar in Fig. 2 and Table 1) should be those most tolerant of such temperatures in the laboratory. Thus, evolutionary divergence in the ability to withstand high temperatures has taken place within Lake Washington.

Evidence for divergence in development rate within the Cedar River was mixed. In other studies, the embryos of early spawners often develop slowest whereas the embryos of late spawners develop fastest, presumably to increase synchrony of developmental events (Tallman 1986; Beacham and Murray 1987, 1988; Brannon 1987). For Lake Washington, Early Cedar and Middle Cedar embryos hatched and emerged after about the same number of days, but Late Cedar embryos required fewer (Fig. 4). Early emergence by Late Cedar embryos in the laboratory was due to accelerated development prior to hatching, and between hatching and emergence (Table 1). Thus, divergence in development rates within the Cedar River

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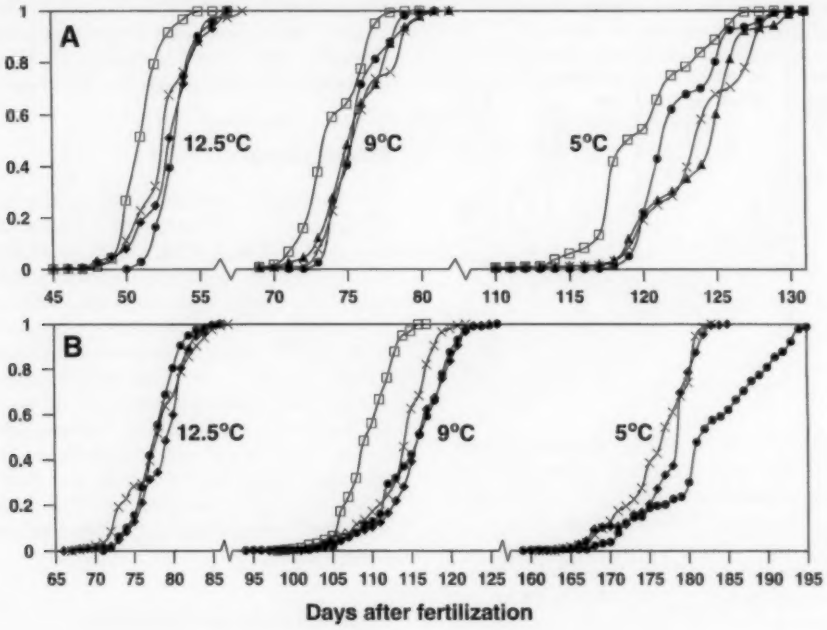
Fig. 4. Cumulative (A) hatching and (B) emergence curves for all fry from each collection at each incubation temperature. Points depict the cumulative proportion of fry that had hatched or emerged on a given day for Early Cedar (solid circles), Middle Cedar (solid triangles), Late Cedar (open squares), and Pleasure Point (crosses). Data were not available for the Late Cedar emergence at 5 or 12.5°C.



was evident for Late Cedar embryos but not for Early Cedar embryos.

Spatial patterns of divergence

The Pleasure Point and Cedar River populations are at least partially reproductively isolated from each other (J.K. Wenburg and A.P. Hendry, unpublished data) and they experience very different incubation environments (Fig. 3). Embryos incubating at Pleasure Point do so in nearly isothermal water (about 10°C) whereas Cedar River embryos incubate in a colder and more variable thermal regime. We tested predictions for divergence between these populations with respect to development rate and yolk conversion efficiency.

Pleasure Point embryos naturally incubate in warmer water than their contemporary Cedar River embryos (Middle Cedar), and hence, the former would be expected to hatch and emerge much earlier in the wild (Fig. 2). We had predicted that the Pleasure Point embryos should therefore delay hatching and emergence to bring their timing closer to the Cedar River peak (sensu Brannon 1987; Tallman and Healey 1991). Contrary to this prediction, hatching and emergence trajectories were nearly identical for Pleasure Point and Middle Cedar embryos at each of the three laboratory temperatures (Fig. 4). In a pilot study 2 years earlier, Pleasure Point embryos also did not delay hatching and emergence relative to Cedar River embryos (Hendry 1995). Divergence in development rate does not appear to have occurred for Pleasure Point and Cedar River embryos beginning incubation at a comparable time.

Embryos from the two locations demonstrated their highest yolk conversion efficiency (i.e., greatest body length at emergence) at laboratory temperatures that corresponded to their natural incubation environments. Similar patterns have been reported in laboratory studies of developmental variation among other sockeye salmon populations (Beacham and Murray 1987, 1989). The matching of yolk conversion efficiency to natural conditions is important because small size and excessive yolk reserves (reflecting incomplete yolk to tissue conversion) increase the susceptibility of newly emerged salmon fry to predators (Taylor and McPhail 1985; Fresh and Schroder 1987). Selection for predator avoidance may be important within Lake Washington because predation rates on sockeye salmon fry can be very high (Beauchamp 1995; Seiler and Kishimoto 1996). Such selection may have led to the evolutionary divergence in yolk conversion efficiency that has taken place within Lake Washington sockeye salmon.

Factors constraining adaptive divergence

The observed divergence in survival rate and yolk conversion efficiency was substantial and has clear fitness advantages. In contrast, the greatest divergence in development rate resulted in only a 6-day difference in time to emergence at 9°C, which would reduce emergence asynchrony only slightly. Other studies comparing embryos that naturally incubate in similar temperatures but at different times have documented greater differentiation. For example, time to yolk absorption for the progeny of different beach spawners from Cultus Lake (lower Fraser River, B.C.) declined by more that 10 days over a 6-week period (at 5°C, Brannon 1987). Similarly, time to emergence differed by about 10 days between embryos of chum salmon (*Oncorhynchus keta*) from Bush Creek (Vancouver Island, B.C.) that spawned a month apart (at about 5°C, Tallman and Healey 1991).

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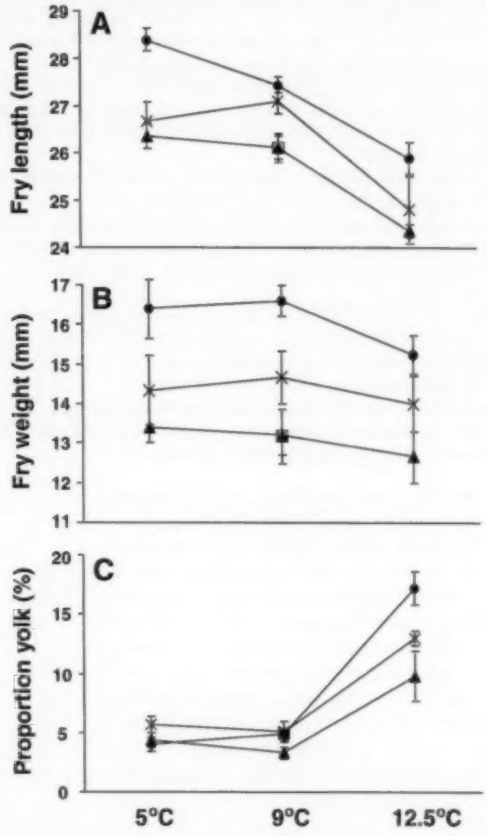
Fig. 5. (A) Fry length, (B) fry weight, and (C) proportion yolk at emergence for Early Cedar (solid circles), Middle Cedar (solid triangles), Late Cedar (open squares), and Pleasure Point (crosses). Error bars represent 1 SE around the mean. Data were not available for Late Cedar at 5 or 12.5°C.



There are several reasons why development rates may not have diverged much despite some restriction on gene flow and large differences in incubation conditions. First, synchronization can also be achieved through spawning time (Brannon 1987), and peak spawning at Pleasure Point is later than in the Cedar River (late November versus late October). This difference has been evident since at least the mid-1960s (Woodey 1966) and would reduce emergence asynchrony between these sites. Second, selection for synchronized emergence may be less strong than in other sockeye salmon lake systems because Lake Washington provides ample feeding opportunities for juveniles throughout the spring (Eggers 1978). The protracted spawning and emergence periods in the Cedar River (Seiler and Kishimoto 1996) may be the result of relaxed selection for synchronized emergence. Third, accelerated development in the Late Cedar embryos may have evolved for avoidance of high spring temperatures rather than for synchronization.

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References

Beacham, T.D., and Murray, C.B. 1987. Adaptive variation in body size, age, morphology, egg size, and developmental biology of chum salmon (*Oncorhynchus keta*) in British Columbia. Can. J. Fish. Aquat. Sci. **44**: 244–261.

Beacham, T.D., and Murray, C.B. 1988. Variation in developmental biology of pink salmon (*Oncorhynchus gorbuscha*) in British Columbia. Can. J. Zool. **66**: 2634–2648.

Beacham, T.D., and Murray, C.B. 1989. Variation in developmental biology of sockeye salmon (*Oncorhynchus nerka*) and chinook salmon (*O. tshawytscha*) in British Columbia. Can. J. Zool. **67**: 2081–2089.

Beauchamp, D.A. 1995. Riverine predation on sockeye salmon fry migrating to Lake Washington. North Am. J. Fish. Manage. **15**: 358–365.

Blair, G.R., Rogers, D.E., and Quinn, T.P. 1993. Variation in life history characteristics and morphology of sockeye salmon in the Kvichak River system, Bristol Bay, Alaska. Trans. Am. Fish. Soc. **122**: 550–559.

Brannon, E.L. 1987. Mechanisms stabilizing salmonid fry emergence timing. Can. Spec. Publ. Fish. Aquat. Sci. No. 96. pp. 120–124.

Eggers, D.M. 1978. Limnetic feeding behavior of juvenile sockeye salmon in Lake Washington and predator avoidance. Limnol. Oceanogr. **23**: 1114–1125.

Fresh, K.L., and Schroder, S.L. 1987. Influence of the abundance, size, and yolk reserves of juvenile chum salmon (*Oncorhynchus keta*) on predation by freshwater fishes in a small coastal stream. Can. J. Fish. Aquat. Sci. **44**: 236–243.

Gharrett, A.J., and Smoker, W.W. 1993. Genetic components in life history traits contribute to population structure. *In* Genetic conservation of salmonid fishes. *Edited by* J.G. Cloud and G.H. Thorgaard. Plenum Press, New York. pp. 197–202.

Gharrett, A.J., and Thomason, M.A. 1987. Genetic changes in pink salmon (*Oncorhynchus gorbuscha*) following their introduction into the Great Lakes. Can. J. Fish. Aquat. Sci. **44**: 787–792.

Hendry, A.P. 1995. Sockeye salmon (*Oncorhynchus nerka*) in Lake Washington: an investigation of ancestral origins, population differentiation and local adaptation. Master's thesis, University of Washington, Seattle, Wash.

Hendry, A.P., and Kinnison, M.T. 1998. Taking time with microevolution. Trends Ecol. Evol. **13**: 76–77.

Hendry, A.P., and Quinn, T.P. 1997. Variation in adult life history and morphology among Lake Washington sockeye salmon (*Oncorhynchus nerka*) populations, in relation to habitat features and ancestral affinities. Can. J. Fish. Aquat. Sci. **54**: 75–84.

Hendry, A.P., Leonetti, F.E., and Quinn, T.P. 1995. Spatial and temporal isolating mechanisms: the formation of discrete breeding aggregations of sockeye salmon (*Oncorhynchus nerka*). Can. J. Zool. **73**: 339–352.

Hendry, A.P., Quinn, T.P., and Utter, F.M. 1996. Genetic evidence for the persistence and divergence of native and introduced sockeye salmon (*Oncorhynchus nerka*) within Lake Washington, Washington. Can. J. Fish. Aquat. Sci. **53**: 823–832.

Huitema, B.E. 1980. The analysis of covariance and alternatives. John Wiley & Sons, Inc., New York.

Jensen, J.O.T. 1988. A microcomputer program for predicting

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embryonic development in Pacific salmon and steelhead trout. World Aquacult. **19**: 80–81.

Kinnison, M., Unwin, M., Boustead, N., and Quinn, T.P. 1998. Population-specific variation in body dimensions of adult chinook salmon (*Oncorhynchus tshawytscha*) from New Zealand and their source population, 90 years after introduction. Can. J. Fish. Aquat. Sci. **55**: 554–563.

Quinn, T.P., Nielsen, J.L., Gan, C., Unwin, M.J., Wilmot, R., Guthrie, C., and Utter, F.M. 1996. Origin and genetic structure of chinook salmon, *Oncorhynchus tshawytscha*, transplanted from California to New Zealand: allozyme and mtDNA evidence. Fish. Bull. U.S. **94**: 506–521.

Reznick, D.N., Shaw, F.H., Rodd, F.H., and Shaw, R.G. 1997. Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). Science (Washington, D.C.), **275**: 1934–1937.

Seiler, D., and Kishimoto, L.E. 1996. Annual report: 1995 Cedar River sockeye salmon fry production evaluation program. (Available from Washington Department of Fish and Wildlife, Olympia, WA 98501-1091, U.S.A.)

Stearns, S.C. 1983. The genetic basis of differences in life-history traits among six populations of mosquitofish (*Gambusia affinis*) that shared ancestors in 1905. Evolution, **37**: 618–627.

Svensson, E. 1997. The speed of life-history evolution. Trends Ecol. Evol. **12**: 380–381.

Tallman, R.F. 1986. Genetic differentiation among seasonally distinct spawning populations of chum salmon, *Oncorhynchus keta*. Aquaculture, **57**: 211–217.

Tallman, R.F., and Healey, M.C. 1991. Phenotypic differentiation in seasonal ecotypes of chum salmon, *Oncorhynchus keta*. Can. J. Fish. Aquat. Sci. **48**: 661–671.

Tallman, R.F., and Healey, M.C. 1994. Homing, straying, and gene flow among seasonally separated populations of chum salmon (*Oncorhynchus keta*). Can. J. Fish. Aquat. Sci. **51**: 577–588.

Taylor, E.B., and McPhail, J.D. 1985. Burst swimming and size-related predation of newly emerged coho salmon *Oncorhynchus kisutch*. Trans. Am. Fish. Soc. **114**: 546–551.

Taylor, E.B., Harvey, S., Pollard, S., and Volpe, J. 1997. Postglacial genetic differentiation of reproductive ecotypes of kokanee *Oncorhynchus nerka* in Okanagan Lake, British Columbia. Mol. Ecol. **6**: 503–517.

Taylor, S.G. 1980. Marine survival of pink salmon fry from early and late spawners. Trans. Am. Fish. Soc. **109**: 79–82.

Thorne, R.E., and Ames, J.J. 1987. A note on variability of marine survival of sockeye salmon (*Oncorhynchus nerka*) and effects of flooding on spawning success. Can. J. Fish. Aquat. Sci. **44**: 1791–1795.

Wood, C.C. 1995. Life history variation and population structure in sockeye salmon. *In* Evolution and the aquatic ecosystem: defining unique units in population conservation. *Edited by* J.L. Nielsen. Am. Fish. Soc. Symp. No. 17. pp. 195–216.

Woodey, J.C. 1966. Sockeye salmon spawning grounds and adult returns in the Lake Washington watershed, 1965. Master's thesis, University of Washington, Seattle, Wash.

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Changes in the quantity and characteristics of large woody debris in streams of the Olympic Peninsula, Washington, U.S.A. (1982–1993)

Michael L. McHenry, Eric Shott, Robert H. Conrad, and Glenn B. Grette

Abstract: We assessed the changes in large woody debris (LWD) abundance and composition at 28 sites in 27 low-gradient Olympic Peninsula streams between 1982 and 1993. The average number of pieces of debris was virtually identical ($P = 0.98$) in both years (50.7 versus 50.6). However, we found a significant ($P \leq 0.01$) reduction in the total volume of LWD material in the stream sites surveyed (51.7 $m^3 \cdot 100\ m^{-1}$ in 1982 to 38.2 $m^3 \cdot 100\ m^{-1}$ in 1993). While the mean volume of second-growth derived LWD increased from 3.6 to 10.9 $m^3 \cdot 100\ m^{-1}$ ($P < 0.01$), the increase was insufficient to offset the loss of old-growth derived LWD. The mean volume of old-growth derived LWD for all sites decreased from 48.1 to 27.4 $m^3 \cdot 100\ m^{-1}$ between sample years ($P < 0.01$). The mean diameter of second-growth derived LWD was significantly larger in 1993 than in 1982, although still smaller than old-growth derived pieces. We measured a significant increase in the percentage of LWD pieces rated as highly decayed from 1982 to 1993. The results indicate that the loss of old-growth derived LWD following the removal of old-growth riparian forests is initially very rapid, followed by a slower rate of depletion associated with watershed destabilization. Inputs of LWD from second-growth riparian forests up to 73 years old were characterized by small diameter, high mobility, and high decay rates.

Résumé : Nous avons évalué les changements, entre 1982 et 1993, dans l'abondance et la composition des gros débris ligneux à 28 sites dans 27 cours d'eau à pente faible de la péninsule Olympic. Les nombres moyens de débris étaient pour ainsi dire identiques ($P = 0{,}98$) dans les deux années (50,7 et 50,6). Cependant, nous avons observé une réduction importante ($P \leq 0{,}01$) du volume total de gros débris ligneux aux sites fluviaux examinés (51,7 $m^3 \cdot 100\ m^{-1}$ en 1982 à 38,2 $m^3 \cdot 100\ m^{-1}$ en 1993). Bien que le volume moyen de gros débris ligneux issus de deuxième venue se soit accru, passant de 3,6 à 10,9 $m^3 \cdot 100\ m^{-1}$ ($P < 0{,}01$), cet accroissement était insuffisant pour compenser la diminution des gros débris ligneux issus de vieux arbres. Le volume moyen de gros débris ligneux issus de vieux arbres pour l'ensemble des sites a diminué, passant de 48,1 à 27,4 $m^3 \cdot 100\ m^{-1}$ entre les années d'échantillonnage ($P < 0{,}01$). Le diamètre moyen des gros débris ligneux issus de deuxième venue était significativement plus grand en 1993 qu'en 1982, mais il était tout de même plus petit que celui des débris issus de vieux arbres. Nous avons mesuré un accroissement significatif du pourcentage de gros débris ligneux considérés comme étant fortement décomposés de 1982 à 1993. Les résultats montrent que la diminution de la quantité de gros débris ligneux issus de vieux arbres par suite de l'élimination des vieilles forêts riveraines est initialement très rapide, et se poursuit ensuite plus lentement en raison d'une déstabilisation du bassin hydrographique. Les gros débris ligneux issus des forêts riveraines de deuxième venue atteignant au plus 73 ans étaient caractérisés par de petits diamètres, une forte mobilité et des taux de décomposition élevés.
[Traduit par la Rédaction]

Introduction

The relationship between riparian management, recruitment of large woody debris (LWD) to stream channels, and the maintenance of healthy stream habitats has received increasing attention during the last two decades (Keller and Swanson 1979; Bisson et al. 1987; Hicks et al. 1991; Abbe and Montgomery 1996). In mountainous watersheds of the Pacific Northwest, conversion of native, mature coniferous forests to tree plantations has had a deleterious effect on habitats used by Pacific salmonids (Frissell 1992; Ralph et al. 1994). Basin-level disturbances from logging, at intervals ranging from 45 to 80 years, have decreased the size (Hartman and Scrivener 1990), amount (Murphy and Koski 1989), and species composition (Veldhuisen 1990) of LWD being recruited to streams in the region. However, relatively little is known concerning the temporal variability of LWD in streams.

On the western Olympic Peninsula of Washington State, the dominant land use in low-elevation zones (<1000 m) is industrial forestry. Coho salmon (*Oncorhynchus kisutch*), because they spend 1–2 years of their lives in freshwater, have been significantly affected by watershed level changes associated with logging (Brown et al. 1994; Washington Department of Fish and Wildlife and Northwest Indian Treaty Tribes 1994). The relationships between modification of riparian vegetation, inputs of LWD, and the maintenance of habitat features used

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by juvenile coho salmon are particularly critical (Murphy et al. 1986; Bilby and Ward 1991; Dolloff 1986).

In this study, we assessed the changes in LWD loading and composition at 28 sites in 27 low-gradient Olympic Peninsula streams over an 11-year period (1982–1993). These sites were first surveyed by Grette (1985) in 1982. Grette (1985) concluded that losses of old-growth derived LWD following logging of riparian forest was 0.5 piece·100 m^{-1}·$year^{-1}$ and that inputs of second-growth derived LWD were inadequate to offset this loss. Other researchers have described similar losses of LWD from streams draining old-growth Pacific Northwest forests following logging (Murphy and Koski 1989). Bilby and Ward (1991) described a much higher loss rate for the first 5 years immediately following logging.

The purpose of this study was to evaluate the precision of these estimates using empirical data and to assess if recent improvements in riparian management are resulting in any detectable changes in LWD recruitment and quality in Olympic Peninsula streams. Because riparian protection strategies are relatively new and evolving rapidly, this information provides an important benchmark for habitat managers. Although we could not evaluate the effectiveness of specific riparian practices, the conditions measured at individual sites represent the result of up to 80 years of various land management practices.

Study site

Twenty-seven streams on the western and northwestern Olympic Peninsula were selected for study (Fig. 1). The majority of the streams were tributaries of the Pysht, Hoko, Dickey, Sol Duc, Hoh, and Queets rivers. Three streams were small, independent tributaries to the Pacific Ocean (Kalaloch, Goodman, and Mosquito creeks). Watersheds in this region are generally mountainous and have elevations ranging from sea level to 2500 m. Study sites were located in low-gradient (<2%) channel reaches at elevations <200 m. Precipitation in the region is heavy (150–400 cm·$year^{-1}$), with the majority falling as rainfall between the months of November and March.

Geologic features of the study area are dominated by sedimentary rocks (sandstones and siltstones) and are often modified by glacial outwash (Tabor and Cady 1978). The vegetative community of the study area is characterized as temperate rainforest. Climax riparian forests are dominated by large (>60 m in height) and old (>300 years) stands of Sitka spruce (*Picea sitchensis*), western redcedar (*Thuja plicata*), and western hemlock (*Tsuga heterophylla*). Second-growth riparian areas in logged basins are often dominated by deciduous trees, especially red alder (*Alnus rubra*) and bigleaf maple (*Acer macrophyllum*).

Methods

Site classification

In Grette's (1985) original survey, 28 sites were assigned to four groups based upon the logging history of the streamside forests. Each group contained seven sites. The groups were old-growth or unlogged sites, young second-growth sites logged 10–26 years prior to 1982, middle-aged second-growth sites logged 27–37 years prior to 1982, and old second-growth sites logged 40–62 years prior to 1982. These sites were located on private, state, and federal lands.

Various levels of protection were applied to the riparian forests of those sites that were logged after the 1982 study. Prior to 1988, Washington State Forest Practice Rules did not require leave trees in riparian zones to provide LWD for fish-bearing channels (shade trees only). As a result, some sites were logged without buffers or with narrow riparian management zones ranging from 7 to 15 m. Between 1982 and 1993, six of the seven original old-growth and two of the old second-growth sites were logged. During this same period, most of the private ownership upstream of the remaining old-growth site at Cold Creek was also logged. Portions of the federal ownership of Cold Creek had also been previously logged with extensive road construction. Other watersheds containing study sites have had extensive upstream logging between sample years and prior to the original study. As a result, extensive watershed disturbances have occurred in all study site watersheds. These events have modified the original study design, particularly the unlogged control group established by Grette (1985). Because of the amount of disturbance at the unlogged sites, we chose to reclassify this group as logged old-growth. This included the Cold Creek site, which, although unlogged, had clearly suffered direct channel disturbance from a landslide just above the study reach. Since the riparian forests were largely intact (two logged with buffers) on the other logging-history groups, we retained their original designations and updated their respective ages. The new logging-history groups were logged old-growth sites (LOG), young second-growth sites logged 21–37 years prior to 1993 (YSG), middle-aged second-growth sites logged 38–48 years prior to 1993 (MASG), and old second-growth sites logged 51–73 years prior to 1993 (OSG).

Survey techniques

Study sites were originally selected based upon gradient, stream order, watershed area, and age of the surrounding riparian forest. Selected physical characteristics of the study streams are depicted in Table 1. A 100-m reach of the stream was selected randomly from a longer reach (600–1000 m) that met the study site criteria. We relocated the original 100-m study sites by finding surviving streamside reference points marked in 1982 and described by compass bearings and distances in the original data set. In both 1982 and 1993, a debris map was prepared during low flows using a planimetric scale system. Variables mapped included low-flow wetted channel, bank-full channel, and position of LWD. LWD included all pieces exposed within the bed or bank with a diameter and length ≥ 10 cm and 3 m, respectively.

Information collected from individual pieces of debris included species, length, diameter, decay class (Table 2), derivation (old-growth or second-growth), relative stability, and a description of position within the channel. Only that portion of an exposed individual piece located within the bank-full channel was measured. Pieces meeting the diameter criteria, embedded in the bed or bank, and >2.0 m in exposed length were also measured and included in the data. Diameter was measured at the large end of an individual piece with calipers. Derivation was determined visually by examining a combination of factors, including species, state of decay, size, and depth of burial.

The only methodological changes between the 1982 and 1993 surveys were the use of multiple survey crews in 1993 and the use of calipers in 1993 versus a meter stick in 1982 to measure LWD diameter. Survey crews were trained by the original investigator and a quality assurance check was made on each crew. To assess differences between LWD measured with a meter stick versus calipers, we compared the diameters of 55 tagged pieces measured in 1982 and 1993 and found no significant difference. We do not believe that the methods used in 1993 biased the results, except where noted in the visual rating of LWD decay classification.

As an additional assurance for consistency between years, we screened both the 1982 and 1993 data sets using standardized criteria for LWD. This resulted in a slight reduction of LWD (<1%) at most sites from the original results reported by Grette (1985). For example, in the original study, Grette (1985) collected information on individual pieces <1 m in length that were embedded in the streambed.

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Fig. 1. Location of the 28 streams used in the study, Olympic Peninsula, Washington, U.S.A.

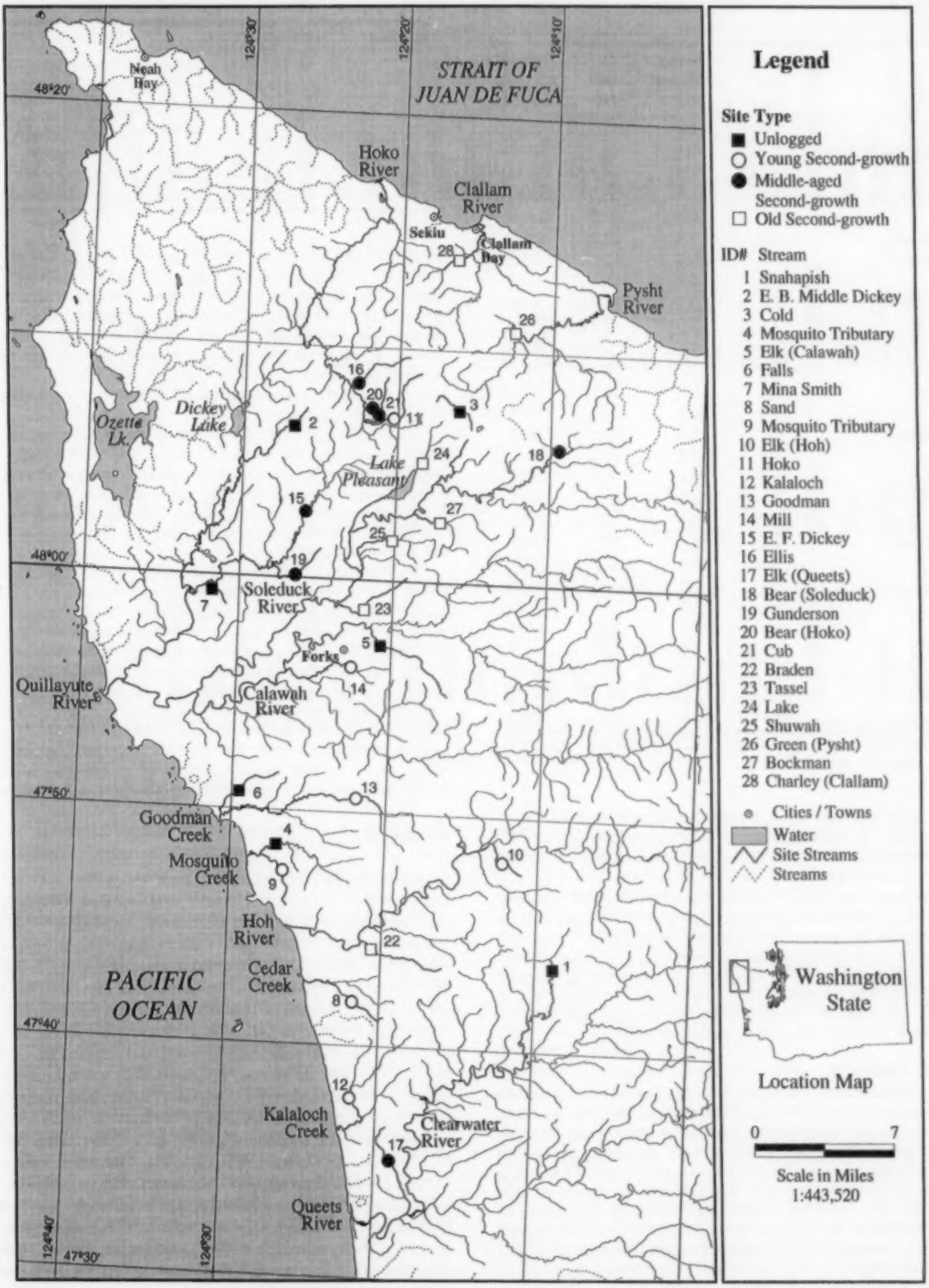

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Table 1. Watershed characteristics and riparian age classification in 1982 of the 28 study streams, Olympic Peninsula, Washington, U.S.A.

Stream	Watershed area (km^2)	Low-flow discharge ($ft^3 \cdot s^{-1}$)	Bank-full width (m)	Riparian age (year logged)
Snahapish	8.0	0.2	12.3	(LOG)
E.B. Middle Dickey	6.2	0.8	10.3	(LOG)
Cold	7.5	1.6	10.3	(LOG)
Elk (Calawah)	8.0	1.4	13.0	(LOG)
Falls	5.7	0.3	10.3	(LOG)
Mina Smith	5.2	0.3	10.7	(LOG)
Mosquito	8.5	0.4	12.2	(LOG)
Sand	5.2	0.8	11.3	1972
Mosquito	8.0	0.3	10.8	1969
Elk (Hoh)	11.7	2.5	7.2	1962
Hoko	8.8	0.4	15.0	1959
Kalaloch	7.5	2.5	9.6	1957
Goodman	8.0	0.3	16.6	1956
Mill	3.4	0.4	7.2	1956
E.F. Dickey	6.5	0.6	12.0	1955
Ellis	9.3	1.1	11.7	1952
Elk (Queets)	5.7	0.6	9.2	1952
Bear (Soleduck)	8.8	0.7	10.4	1950
Gunderson	8.0	0.4	8.9	1950
Bear (Hoko)	9.8	2.4	10.3	1945
Cub	5.2	0.4	10.4	1945
Braden	8.5	0.2	9.9	1942
Tassel	6.2	1.0	7.1	(1937)
Lake	8.0	1.1	10.6	1930
Shuwah	9.1	1.0	14.7	1930
Green	12.4	0.5	15.4	1930
Bockman	7.5	0.8	16.1	(1920)
Charley	10.4	0.2	15.7	1920

Note: Riparian age data in parentheses indicate that the site was logged between 1982 and 1993.

Additionally, rootwads with and without attached boles and live trees were included in the 1982 database. The screen omitted rootwads without attached boles and live trees, thus ensuring that the analysis was consistent between years.

Volumes of individual debris pieces were calculated using the equation for a cylinder ($\pi \times \text{radius}^2 \times \text{length}$) for all old-growth pieces and second-growth pieces <8 m in length (Grette 1985). For second-growth pieces >8 m long, a taper factor of 8.0 $mm \cdot m^{-1}$ was applied (Grette 1985). The length of the piece was multiplied by the taper factor to determine the diameter of the small end of the piece. The butt diameter and small-end diameter were then averaged and half this value was used as the radius in the volume calculation.

Statistical analyses

The total number and volume of LWD pieces measured at each site were calculated for the 1982 and 1993 surveys. This was also done for the derivation categories that each piece was assigned to: old-growth derived and second-growth derived. Since the same 100-m stream sections were surveyed in both years, the 2 years of LWD data for each stream were treated as matched pairs and paired sample *t*-tests were used to test for between-year differences. The change in number of pieces and volume of total LWD, old-growth derived LWD, and second-growth derived LWD relative to 1982 was calculated for each site.

We also examined whether there were differences among the four logging-history groups for the changes in LWD parameters from 1982 and 1993. Single-factor analysis of variance (ANOVA) was used to test for among-group differences. Before conducting the ANOVA tests, the data were tested for homogeneity of group variances using Levene's test (Milliken and Johnson 1992) to ensure the appropriateness of the test. Fisher's least significant difference (LSD) multiple comparison procedure (Milliken and Johnson 1992) was used to test for differences between all possible group pairs when an ANOVA was significant ($P \leq 0.10$).

Mean diameters of old-growth derived and second-growth derived LWD pieces were compared between 1982 and 1993 at each sample site. Independent sample *t*-tests were used to test for between-year differences in mean diameters. The results of Levene's test for homogeneity of group variances were used to determine whether the separate or pooled standard error of the difference in means was used to calculate the *t*-statistic.

We compared the condition of second-growth LWD in 1982 with that in 1993 by comparing the distributions of second-growth derived pieces among the decay class categories. For this analysis, we combined the seven original decay class categories that the data were classified to during 1982 and 1993 into three broader categories (Table 2). This was done to reduce observer variation in LWD decay classification, as we were confident that observers could make accurate calls based upon general LWD condition (i.e., presence or absence of bark) versus the finer distinction required to classify pieces into the original seven categories. Fisher's exact test (Conover 1980) was used to compare the distributions of second-growth derived LWD pieces among the three condition categories in the two years.

Table 2. Description of debris decay classes used by Grette (1985) and modified to reduce observer bias for this study.

1982 class	1993 class	Description
1	1	Bark intact, limbs present
2	1	Bark intact, limbs absent
3	2	Bark loose or absent
4	2	Bark absent, surface slightly rotten
5	3	Surface extensively rotted
6	3	Surface rotted, center solid
7	3	Surface rotted, center rotted

Results

Comparison of 1982 and 1993 data

Between the 1982 and 1993 surveys, the total volume of LWD decreased at 20 of 28 sites (Fig. 2A). The mean volume of LWD decreased 13.5 m^3 (SD = 20.9) from 51.7 m^3 in 1982 to 38.2 m^3 in 1993 (values for volume and numbers of LWD are per 100 m of stream). Twenty-two of the 28 sites had a decrease in the volume of old-growth derived LWD (Fig. 2B). The mean volume of old-growth derived LWD for all sites decreased 20.7 m^3 (SD = 22.0) from 48.1 m^3 in 1982 to 27.4 m^3 in 1993. The decreases in mean LWD volume and mean old-growth derived LWD volume were both significant (paired sample *t*-test; $P < 0.01$). In contrast, 27 of 28 sites had an increase in the volume of second-growth derived LWD debris between 1982 and 1993 (Fig. 2C). The mean volume of second-growth derived LWD increased 7.3 m^3 (SD = 5.4) from 3.6 m^3 in 1982 to 10.9 m^3 in 1993. The increase in mean volume of second-growth derived LWD was significant (paired sample *t*-test; $P < 0.01$). However, the increase in second-growth derived LWD did not offset the loss of old-growth derived LWD at most sites. At only two of the 22 sites

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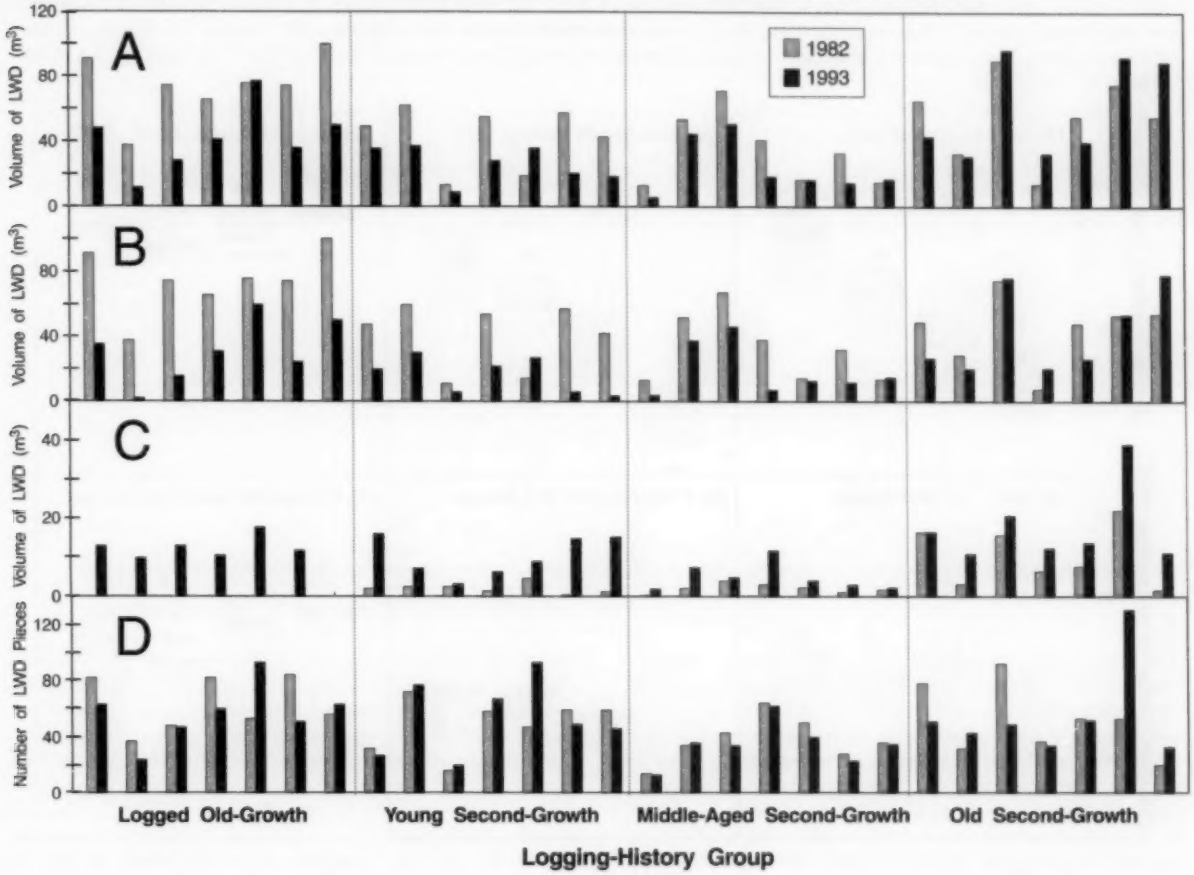
Fig. 2. Comparison of 1982 and 1993 values of (A) total volume of LWD, (B) volume of old-growth derived LWD, (C) volume of second-growth derived LWD, and (D) number of LWD pieces for the 28 sites surveyed ordered by logging-history group.



that had a decrease in old-growth derived LWD volume was the increase in volume of second-growth derived LWD greater than the decrease in volume of old-growth derived LWD.

In contrast with volume, the mean numbers of LWD pieces per site were virtually identical for the 1982 and 1993 surveys, 50.7 and 50.6, respectively. Although 10 of the 28 sites had a greater number of LWD pieces in 1993 than in 1982 (Fig. 2D), the difference in mean number of pieces was not significant (paired sampled *t*-test; $P = 0.98$). The mean number of old-growth derived LWD pieces decreased from 36.8 to 17.5, while the mean number of second-growth derived LWD pieces increased from 13.7 to 33.1 between 1982 and 1993. Both these changes were significant (paired sample *t*-test; $P < 0.01$). The numbers of LWD pieces and LWD volumes for individual survey sites for 1982 and 1993 are given in the Appendix.

Differences among groups for changes in LWD

There were significant differences among groups for the change in mean LWD volume from 1982 to 1993 (ANOVA; $P < 0.01$). Only the OSG group had a positive mean percent change in total LWD volume (+5.3 m^3). The other three logging-history groups had mean decreases in total LWD volume of −11 m^3 or more (Fig. 3A). Fisher's LSD tests indicated that the mean changes in total LWD volume for the LOG and OSG groups were significantly different from each other and from the other two groups ($P < 0.10$) but the YSG and MASG groups were not significantly different from each other ($P = 0.54$). Differences in LWD piece counts were not as significant as those for LWD volume. Mean changes in the total number of LWD pieces from 1982 to 1993 ranged from −6 to +5 among the four groups (Fig. 3B). There was not a significant difference among the four groups for the mean change in the number of LWD pieces (ANOVA; $P = 0.80$)

There were significant among-group differences for the changes in total volume of old-growth derived LWD from 1982 to 1993 (ANOVA; $P < 0.01$). The OSG group had the smallest mean decrease in the volume of old-growth derived LWD volume (−1.8 m^3). The other three logging-history groups had mean decreases in volume of old-growth derived LWD of −14 m^3 or more (Fig. 3C). Fisher's LSD tests indicated that the mean change in volume of old-growth derived LWD for the LOG group was significantly different from that of the other three logging-history groups ($P < 0.05$). The YSG and MASG groups were not significantly different from each

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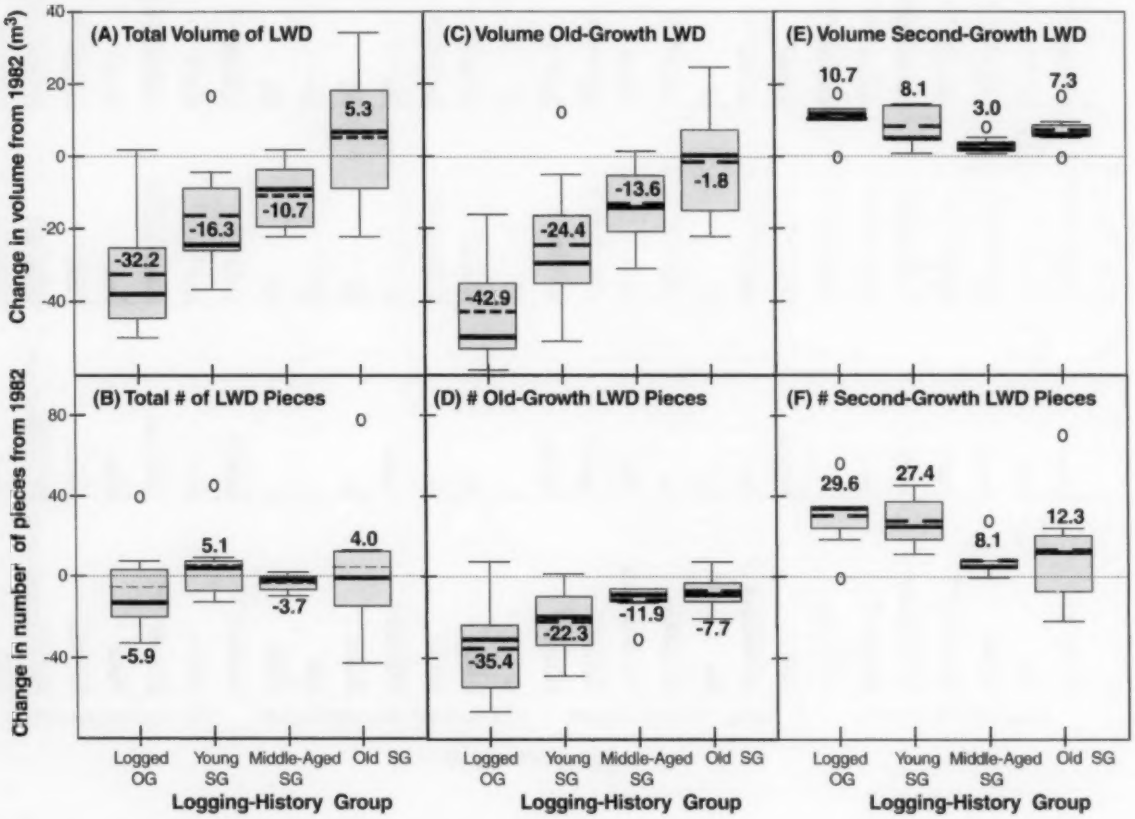
Fig. 3. Box plots showing the change from 1982 in (A) total volume and (B) total number of LWD pieces, (C) total volume and (D) total number of old-growth derived LWD pieces, and (E) total volume and (F) total number of second-growth derived LWD pieces for each logging-history group. Box plots show median value (heavy solid line), mean value (heavy broken line), the central 50% of the data (shaded area indicates the 25th and 75th percentiles), and the lowest and highest observed values that are not considered outliers (box whiskers). Data values more than 1.5 box lengths from the edge of the box are considered extreme and are marked by a circle. The mean value for each group is shown in or near the box.


(A) Total Volume of LWD
(C) Volume Old-Growth LWD
(E) Volume Second-Growth LWD
(B) Total # of LWD Pieces
(D) # Old-Growth LWD Pieces
(F) # Second-Growth LWD Pieces
Change in volume from 1982 (m³)
Change in number of pieces from 1982
Logged OG
Young SG
Middle-Aged SG
Old SG
Logging-History Group

other ($P = 0.24$) as were the MASG and OSG groups ($P = 0.20$). Mean changes in the number of old-growth derived LWD pieces from 1982 to 1993 ranged from –8 to –35 for the four groups (Fig. 3D). There was also a significant difference among groups in the mean change in the number of pieces of old-growth derived LWD (ANOVA; $P = 0.03$). Fisher's LSD tests indicated that the only significant differences were between the LOG group and the MASG and OSG groups ($P < 0.02$).

There were also significant among-group differences for the change in total volume of second-growth derived LWD from 1982 to 1993 (ANOVA; $P = 0.05$). The MASG group had the smallest mean increase in second-growth derived LWD (+3.0 m^3). The other three logging-history groups had mean increases in volume of second-growth derived LWD of 7 m^3 or more (Fig. 3E). Fisher's LSD tests indicated that the mean change in volume of second-growth derived LWD for the MASG group was significantly different from that of the LOG and YSG logging-history groups ($P < 0.10$). No other significantly different pairs were found (all $P > 0.10$). Mean changes in the number of second-growth derived LWD pieces from 1982 to 1993 ranged from +8 to +30 for the four groups (Fig. 3F). There was not a significant difference among the groups for the mean change in the number of second-growth derived LWD pieces (ANOVA; $P = 0.12$).

Annual rates of change in LWD

Mean annual rates of change in total volume of LWD or number of LWD pieces and mean annual percent rate of change from 1982 values are summarized for total, old-growth derived, and second-growth derived LWD by logging-history group in Table 3. There were gradual decreases in the mean annual rates of decline for both the volume and number of old-growth derived pieces among the groups. The LOG group had the largest mean annual rates of change (–3.9 $m^3 \cdot 100\ m^{-1} \cdot year^{-1}$ and –3.2 pieces$\cdot 100\ m^{-1} \cdot year^{-1}$) and the OSG had the smallest (–0.2 $m^3 \cdot 100\ m^{-1} \cdot year^{-1}$ and –0.7 pieces$\cdot 100\ m^{-1} \cdot year^{-1}$). When the rates are expressed as percent change from 1982 values, these trends are not as consistent. The OSG group had a positive mean annual percent change in the volume of old-growth derived LWD; the mean annual

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Table 3. Mean annual rates of change in volume of LWD and number of pieces of LWD by logging-history group.

Logging-history group	Mean annual change				Mean percent annual change from 1982 values			
	Volume (m^3)		No. of pieces		Volume (m^3)		No. of pieces	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Total LWD								
LOG	–2.9	1.6	–0.5	2.2	–4.1	2.1	–0.5	3.7
YSG	–1.5	1.6	0.5	1.8	–2.3	4.8	1.2	3.8
MASG	–1.0	0.9	–0.3	0.4	–2.6	2.6	–0.9	0.9
OSG	0.5	1.8	0.4	3.5	2.0	5.3	2.0	6.1
Combined	–1.2	1.9	0.0	2.2	–1.7	4.4	0.5	4.0
Old-growth derived LWD								
LOG	–3.9	1.4	–3.2	2.3	–5.5	2.1	–4.9	3.1
YSG	–2.2	1.9	–2.0	1.8	–4.0	5.6	–5.3	3.5
MASG	–1.2	1.0	–1.1	0.8	–3.6	3.1	–4.3	2.1
OSG	–0.2	1.6	–0.7	0.8	1.3	6.9	–3.2	2.7
Combined	–1.9	2.0	–1.8	1.8	–3.0	5.2	–4.4	2.8
Second-growth derived LWD								
LOG	1.0	0.5	2.7	1.6	na		na	
YSG	0.7	0.5	2.5	1.2	76.4	106.7	22.8	14.7
MASG	0.3	0.3	0.7	0.8	19.6	19.8	11.9	19.2
OSG	0.7	0.5	1.1	2.8	14.6	19.1	8.5	12.0
Combined	0.7	0.5	1.8	1.9	36.8	66.8	14.4	16.1

Note: The percent change from 1982 cannot be calculated for second-growth derived LWD in the LOG group because no second-growth derived LWD was present in the initial 1982 survey of this group.

percent change in the number of old-growth derived pieces is similar for all four groups, ranging from –3.2 to –5.3%.

The mean annual rates of change in second-growth derived LWD relative to 1982 were also estimated for sites in the YSG, MASG, and OSG logging-history groups. Except for the MASG group, increases in second-growth LWD averaged nearly 1 $m^3 \cdot 100\ m^{-1} \cdot year^{-1}$. Expressed as a percentage, trends were more significant. The YSG group had a much greater increase in the volume of second-growth derived LWD (+76.4%) compared with the MASG and OSG groups, +19.6 and +14.6%, respectively (Table 3). However, there was a large degree of within-group variability for the YSG group (CV for group mean = 107%). The differences between the YSG and other second-growth groups for the mean rate of increase in the number of second-growth LWD pieces were not as great (Table 3); mean rates of change were +22.8, +11.9, and +8.5% for the YSG, MASG, and OSG groups, respectively.

Mean diameters of LWD pieces

Diameters of old-growth derived LWD pieces were generally larger than diameters of second-growth derived LWD pieces (Fig. 4). The median diameters of old-growth derived LWD pieces for all four logging-history groups were >0.3 m in both 1982 and 1993 (largest pieces to 2.5 m). In contrast, the median diameters of all second-growth derived LWD pieces were substantially <0.3 m (with one exception, the largest pieces <1.0 m) for all four logging-history groups in both 1982 and 1993 (Fig. 4).

The mean diameters of all old-growth derived LWD pieces are summarized by sample site and year in Table 4. For old-growth derived LWD pieces, only the LOG group had multiple sites where there was a significant difference in mean diameters between 1982 and 1993 (paired *t*-tests; $P \leq 0.10$). The mean diameter in 1993 was larger than the mean diameter in 1982 for four of the five sites with a significant difference.

The mean diameters of all second-growth derived LWD pieces are summarized by sample site and year in Table 5. There were four or more sites with significant between-year differences in both the YSG and OSG groups (paired *t*-tests; $P \leq 0.10$). At all of these sites but one, the mean diameter in 1993 was greater than that in 1982. The magnitude of diameter increases was greatest for the YSG sites (>10 cm) but less for the MASG and OSG sites (generally <10 cm).

Decay class condition of second-growth derived LWD

In general, second-growth derived LWD pieces sampled in 1993 were in a more advanced state of decay than those sampled in 1982 for every logging-history group. We observed a shift in the frequency distributions of pieces classified in decay classes 1–4 in 1982 to those of decay classes 5–7 in 1993. At all sites but two, there was an increase in the percentage of LWD pieces classified into decay class category 5, 6, or 7 (Table 6). At 11 of these 19 sites (excluding the LOG group), the increases were significant (Fisher's exact test; $P \leq 0.10$). The trend was most obvious at the YSG sites where in 1987, only 7.8% of the LWD were classified in an advanced state of decay. By 1993, this category increased to 47.9% of the pieces ($P < 0.01$).

Discussion

Forestry practices, including the conversion of old-growth coniferous riparian forests to young stands of deciduous species, instream salvage, and stream cleanout, have altered LWD characteristics of Olympic Peninsula streams. The loss of

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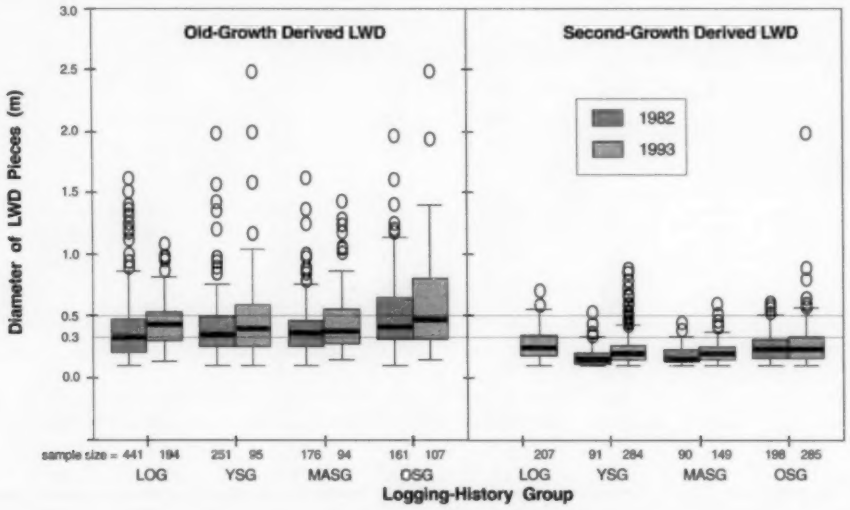
Fig. 4. Box plot showing diameters of old-growth and second-growth derived LWD pieces for each logging-history group in 1982 and 1993. Box plots show median value (heavy solid line), mean value (heavy broken line), the central 50% of the data (shaded area indicates the 25th and 75th percentiles), and the lowest and highest observed values that are not considered outliers (box whiskers). Data values more than 1.5 box lengths from the edge of the box are considered extreme and are marked by a circle. The mean value for each group is shown in or near the box.



LWD from streams bordering old-growth forests that have been logged is particularly rapid: we observed a mean reduction of 58% in old-growth derived LWD volume for all seven old-growth sites that were logged between 1982 and 1993.

The results differ from models of LWD depletion proposed by Grette (1985) and Murphy and Koski (1989). Using data from sites in the YSG, MASG, and OSG groups, Grette (1985) predicted a decline in the number of old-growth derived LWD pieces of 0.5 piece·100 m^{-1}·$year^{-1}$. Between 1982 and 1993, we observed mean rates of decline that were greater and differed by logging-history group. There was a correlation between the years since logging and the loss of old-growth pieces. The most recently logged sites (LOG) had the largest mean rate of decline, 3.2 pieces·100 m^{-1}·$year^{-1}$. This was followed by 2.0 pieces·100 m^{-1}·$year^{-1}$ for the YSG group, 1.1 pieces·100 m^{-1}·$year^{-1}$ for the MASG group, and 0.7 piece·100 m^{-1}·$year^{-1}$ for the OSG group. Only the mean rate for the OSG group, the group with the longest period of time since impact from logging, was close to those predicted by Grette (1985).

In southwest Washington streams, Bilby and Ward (1991) found that the majority of old-growth derived LWD was lost within 5 years immediately following logging. The magnitude of loss increased with stream size. Losses of LWD were reported as 22, 47, and 86% 5 years following harvest for channels 5, 10, and 15 m in width, respectively. Our study sites averaged 10 m in width; therefore, our loss rate is consistent with Bilby and Ward (1991). The total loss of LWD volume was much greater in Olympic Peninsula streams than in those of southwest Washington. Bilby and Ward (1991) reported a prelogging average of 32.3 m^3·100 m of $stream^{-1}$ as opposed to 74.9 m^3·100 m^{-1} in this study. The disparity between volume estimates for unlogged forests may result from ecological differences between study sites. Bilby and Ward (1991) used unlogged sites primarily from the Cascade Mountains at significantly higher elevations than those used in this study.

The results support the concept of a catastrophic loss of LWD following logging. The exact mechanism of this loss is unclear, although three independent and synergistic explanations are plausible: (*i*) direct loss due to destabilization during logging and yarding, (*ii*) channel destabilization and subsequent transport, and (*iii*) long-term decay processes. We found the highest loss rate of old-growth derived LWD in the group most recently impacted by logging (LOG), although loss rates remained high in the YSG and MASG groups as well. This implies that debris loss in Olympic Peninsula streams is strongly related to both initial logging disturbance and channel disturbance associated with watershed-level impacts.

The rapid loss of LWD from streams may be related to flooding and decreased residence time of wood and sediment in channels modified by intensive logging. Hartman and Scrivener (1990) found that prior to logging, little movement or change in LWD abundance was detected in Carnation Creek, British Columbia. Following logging, total volume decreased by 30%. In southeastern Alaskan streams, Bryant (1985) reported destablized logjams that migrated in a downstream direction following logging. Similar changes were observed by Ralph et al. (1994) in an analysis of channel morphology in logged and unlogged basins in Washington State. The authors noted a reduction in LWD size and altered distribution in intensively harvested basins: woody debris was strongly distributed towards stream margins and outside the low-flow wetted width.

Based upon the comparison of the 1982 and 1993 channel maps, we conclude that active movement of LWD has occurred in our study streams. This implies instability, particularly when LWD is composed of small-diameter pieces recruited from young riparian forests. This observation is

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Table 4. Mean diameter, SD, and number of pieces of LWD measured (n) for old-growth derived LWD at each site in 1982 and 1993 and the significance of the t-test comparing the diameters between years (P).

Logging-history group and stream No.	1982 Mean (m)	1982 SD	1982 n	1993 Mean (m)	1993 SD	1993 n	P
LOG							
1	0.390	0.265	82	0.504	0.210	29	**0.04**
2	0.399	0.231	37	0.380	0.108	6	0.75
3	0.414	0.287	47	0.406	0.160	17	0.89
4	0.352	0.188	82	0.471	0.219	26	**0.01**
5	0.368	0.202	53	0.458	0.173	36	**0.03**
6	0.386	0.242	84	0.544	0.144	17	**0.01**
7	0.432	0.267	56	0.358	0.159	63	**0.07**
YSG							
8	0.567	0.378	22	1.300	0.424	2	—[a]
9	0.452	0.270	53	0.450	0.374	33	0.98
10	0.559	0.377	11	0.538	0.230	4	—[a]
11	0.440	0.328	42	0.363	0.167	29	0.25
12	0.421	0.179	21	0.482	0.477	22	0.59
13	0.332	0.221	52	0.857	0.281	3	—[a]
14	0.394	0.230	50	0.965	0.092	2	—[a]
MASG							
15	0.502	0.181	13	0.483	0.325	6	0.90
16	0.453	0.307	22	0.448	0.332	16	0.97
17	0.571	0.344	30	0.632	0.360	18	0.56
18	0.373	0.149	41	0.357	0.134	11	0.75
19	0.317	0.128	31	0.398	0.178	22	**0.09**
20	0.394	0.387	16	0.833	0.442	3	—[a]
21	0.342	0.157	24	0.424	0.238	18	0.21
OSG							
22	0.553	0.329	20	0.675	0.382	8	0.40
23	0.377	0.291	14	0.566	0.299	5	0.23
24	0.525	0.285	40	0.726	0.263	19	**0.01**
25	0.406	0.142	11	0.555	0.241	8	0.15
26	0.457	0.253	35	0.505	0.287	22	0.52
27	0.436	0.261	31	0.513	0.462	38	0.41
28	0.780	0.547	10	0.936	0.790	7	0.64

Note: Significant results ($P \leq 0.10$) are indicated by bold type.

[a]Significance tests are not conducted unless five or more pieces are sampled in each year.

Table 5. Mean diameter, SD, and number of pieces of LWD measured (n) for second-growth derived LWD at each site in 1982 and 1993 and the significance of the t-test comparing the diameters between years (P).

Logging-history group and stream No.	1982 Mean (m)	1982 SD	1982 n	1993 Mean (m)	1993 SD	1993 n	P
LOG							
1			0	0.286	0.121	34	
2			0	0.292	0.138	18	
3			0	0.260	0.121	30	
4			0	0.262	0.113	34	
5			0	0.245	0.094	57	
6			0	0.283	0.118	34	
7			0			0	
YSG							
8	0.170	0.085	10	0.384	0.243	25	**<0.01**
9	0.174	0.059	19	0.186	0.077	44	0.51
10	0.304	0.185	5	0.189	0.093	16	0.24
11	0.140	0.049	16	0.189	0.046	38	**<0.01**
12	0.183	0.087	26	0.175	0.062	71	0.63
13	0.127	0.025	7	0.281	0.132	46	**<0.01**
14	0.175	0.076	9	0.272	0.142	44	**<0.01**
MASG							
15	0.230		1	0.233	0.124	7	—[a]
16	0.192	0.101	12	0.234	0.107	20	0.28
17	0.216	0.099	13	0.255	0.122	16	0.37
18	0.187	0.074	23	0.204	0.087	51	0.44
19	0.169	0.045	19	0.233	0.064	18	**<0.01**
20	0.137	0.041	12	0.181	0.051	20	**0.01**
21	0.170	0.086	12	0.169	0.049	17	0.98
OSG							
22	0.223	0.104	58	0.262	0.104	43	**0.07**
23	0.180	0.110	14	0.249	0.125	38	**0.07**
24	0.252	0.106	52	0.362	0.337	30	**0.09**
25	0.208	0.079	26	0.292	0.113	26	**<0.01**
26	0.258	0.125	18	0.285	0.186	30	0.59
27	0.351	0.133	22	0.250	0.137	93	**<0.01**
28	0.208	0.089	10	0.236	0.110	26	0.48

Note: Significant results ($P \leq 0.10$) are indicated by bold type.

[a]Significance tests are not conducted unless five or more pieces are sampled in each year.

consistent with Heimann's (1988) observation that mobility of LWD increased following logging in Oregon streams. In our study streams, only very large pieces (>80 cm in diameter and >10 m in length) were resistant to movement. These large pieces also proved highly effective in trapping other smaller, more mobile pieces of LWD (forming logjams) that otherwise might have been transported out of the system. This observation supports the concept of a minimum functional size of LWD, referred to as a "key piece", based upon channel width (Washington Forest Practices Board 1995).

Streams draining the western Olympic Peninsula are subjected to tremendous hydrologic stress. To assess the effects of floods on LWD, we analyzed flow records from U.S. Geological Survey gauging stations on the Hoh (1960–1993) and Queets (1930–1991) rivers. The period of study (1982–1993) yielded six of 15 (40%) and six of 13 (46%) of the highest recorded peak flows, respectively, for the Hoh and Queets rivers. Additionally, the largest peak flow for both systems was recorded during a November 1990 flood. The estimated recurrence level for this flood is 25 years for the Hoh and 50 years for the Queets. As smaller debris now dominates the total LWD load, greater transport and higher loss rates may be expected to occur from floods of equal recurrence intervals than in unmanaged conditions.

Depletion of LWD from Pacific Northwest rivers has long-term implications for the productivity of these systems. Mountain channels in the Pacific Northwest are very sensitive to LWD loading. Montgomery et al. (1995) showed that pool spacing in low-gradient channels depleted of LWD is considerably lower than the expected range of 5–7 pools·channel

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Table 6. Distribution of second-growth derived LWD pieces among decay class categories at each site in 1982 and 1993 and the significance of Fisher's exact test comparing the distributions between years (P).

Logging-history group and stream No.	% by decay class, 1982				% by decay class, 1993				
	1–2	3–4	5–7	n	1–2	3–4	5–7	n	P
LOG									
1				0	0.0	41.2	58.8	34	
2				0	11.2	44.4	44.4	18	
3				0	17.2	27.6	55.2	29	
4				0	20.6	55.9	23.5	34	
5				0	22.8	47.4	29.8	57	
6				0	23.5	50.0	26.5	34	
7				0				0	
Combined				0	17.0	45.1	37.9	206	
YSG									
8	50.0	50.0	0.0	10	12.5	4.0	84.0	25	**<0.01**
9	44.4	50.0	5.6	18	14.0	46.5	39.5	43	**<0.01**
10	40.0	40.0	20.0	5	37.5	25.0	37.5	16	—[a]
11	26.7	73.3	0.0	15	24.3	62.2	13.5	37	0.41
12	27.0	61.5	11.5	26	16.9	59.2	20.9	71	0.31
13	71.4	28.6	0.0	7	15.2	4.3	80.5	46	—[a]
14	44.4	33.3	22.3	9	13.6	13.6	72.8	44	—[a]
Combined	38.9	53.3	7.8	90	17.4	34.7	47.9	282	**<0.01**
MASG									
15		100.0		1	14.3	0.0	85.7	7	—[a]
16	16.7	83.3	0.0	12	30.0	65.0	5.0	20	0.65
17	41.7	58.3	0.0	12	12.5	6.2	81.3	16	**<0.01**
18	52.2	39.1	8.7	23	68.6	11.8	19.6	51	**0.03**
19	31.6	52.6	15.8	19	16.6	27.8	55.6	18	**0.05**
20	25.0	75.0	0.0	12	60.0	15.0	25.0	20	**<0.01**
21	27.3	63.6	9.1	11	17.6	58.9	23.5	17	0.75
Combined	34.4	58.9	6.7	90	41.6	25.5	32.9	149	**<0.01**
OSG									
22	45.6	47.4	7.0	57	14.0	23.2	62.8	43	**<0.01**
23	23.1	76.9	0.0	13	10.8	24.3	64.9	37	**<0.01**
24	23.5	62.8	13.7	51	3.3	43.3	53.4	30	**<0.01**
25	34.6	61.6	3.8	26	26.9	46.2	26.9	26	**0.08**
26	33.3	50.0	16.7	18	43.3	43.3	13.4	30	0.78
27	59.1	40.9	0.0	22	25.8	51.6	22.6	93	**<0.01**
28	20.0	60.0	20.0	10	38.5	53.8	7.7	26	0.44
Combined	36.1	55.3	8.6	197	22.8	41.8	35.4	285	**<0.01**

Note: Significant results ($P \leq 0.10$) are indicated by bold type.
[a]Insufficient sample size.

width^{-1} predicted by geomorphic theory (Leopold et al. 1964). Severe depletion of LWD from low-gradient channel types may lead to a reduction or complete loss of pools depending upon gradient (Montgomery et al. 1995). Anadromous salmonids that complete their life history without pools will do so at a much reduced survival rate (Reeves et al. 1988). LWD depletion from higher gradient channels may reduce channel sediment storage (Swanson and Lienkaemper 1978; Montgomery et al. 1996) and affect how terrestrial-derived nutrients are stored and processed (Triska et al. 1982). Loss of LWD also has implications for channel stability in Pacific Northwest stream systems. Smith et al. (1993) showed that the experimental removal of LWD in an Alaskan stream channel caused an immediate redistribution of bed sediments through scour and fill processes.

There was no pattern of contribution of LWD from second-growth riparian forests to stream channels. All logging-history groups gained both in mean volume and number of second-growth derived pieces between 1982 and 1993. There was no apparent trend in the rate of second-growth LWD contribution with age of the adjacent riparian stands. Indeed, the greatest gain was observed for the LOG sites, while the smallest gain was for the MASG sites (Table 3). Heimann (1988) found that preharvest LWD accounted for the majority of debris for up to 140 years in logged Oregon streams. Postdisturbance deciduous LWD increased through 65 years and then decreased. Post-

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disturbance coniferous debris was first detected at 28 years, and volume increased from 28 to 140 years following disturbance.

For the age of second-growth forests examined (<73 years old), recruited LWD was of insufficient size to be retained. Although we measured increases in mean LWD diameter at the majority of sites, there was no apparent influence of the age of the adjacent riparian forests. The average diameter of second-growth derived pieces in 1993 was 0.25 m (SD = 0.14) for all sites. For western Washington stream channels between 11 and 15 m in bank-full width, the minimum recommended diameter for functional pieces of LWD is 0.65 m (Washington Forest Practices Board 1995).

There was a significant increase in the percentage of pieces considered moderately and highly decayed for the YSG, MASG, and OSG logging-history groups between 1982 and 1993. This likely is a direct result of the small-diameter deciduous trees dominating streamside forests. Deciduous species of trees (which comprised ~50% of the debris in 1993) are particularly susceptible to fracture and transport. The rapid breakdown of deciduous species is related to a lower carbon to nitrogen ratio relative to conifers and subsequently to rapid microbial colonization (Bird and Kaushik 1983).

We conclude that the characteristics of LWD from second-growth riparian forests are much different from those associated with late successional coniferous forests. The results of this study and others (Andrus et al. 1988; Heiman 1988; Bilby and Ward 1991) demonstrate that the effects of logging on LWD characteristics of streams are manifested far into the future. Since riparian protection rules are a relatively recent phenomenon in Washington State (1982), the majority of riparian forests on state, private, and some federal lands have been logged at least once. The vegetation of many streamside forests is now dominated by monotypic stands of red alder. A recent analysis of riparian stand conditions on the Hoko River watershed (in which four sites in this study were located) indicated that 93% of the forests bordering salmon-bearing streams were predominantly red alder (Pentec Environmental 1996). Research from coastal Oregon (Emmingham and Hibbs 1996) indicates that conifer succession in alder-dominated forests may be effectively precluded without human intervention (brush control and planting).

These data and the results of this study lead us to conclude that the majority of streams on the Olympic Peninsula will not recover for well over a century or possibly longer. The conditions and land-use history on the Olympic Peninsula are representative of the Pacific Northwest. The implications for salmonid habitat, populations, and resource value are not encouraging. Degraded habitats will continue to produce at levels below their full capacity, while other habitats will decline in quality.

We suggest that protection and restoration of debris loads in streams will require a range of management activities based upon the existing channel and riparian forest characteristics. Active management may be necessary to accelerate large-diameter, conifer-derived LWD for streams with depleted debris loads and deciduous-dominated riparian areas. Streams with adequate instream debris loads and deciduous riparian areas may also require management to ensure long-term recruitment of LWD. Active management could include protection of existing conifer trees within riparian zones, partial cutting of deciduous tree species combined with planting of conifers, placement of debris, or other site-specific activities.

Successful application of management will be dependent upon cooperation among competing interests. The focus of flexible management must be based upon ecological succession to achieve a desired future habitat condition for the stream over the long term. An important element of this cooperation will be providing incentives for voluntary industry cooperation. Watershed analysis, conducted as part of forest management planning, could be used as a vehicle for identifying proper tradeoffs for encouraging industry participation in active stream habitat management in streams of greatest importance to the fisheries resource.

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References

Abbe, T., and Montgomery, T. 1996. Large woody debris jams, channel hydraulics and habitat formation in large rivers. Regul. Rivers, **12**: 201–221.

Andrus, C.W., Long, B.A., and Froehlich, H.A. 1988. Woody debris and its contribution to pool formation in a coastal stream 50 years after logging. Can. J. Fish. Aquat. Sci. **45**: 2080–2086.

Bilby, R.E., and Ward, J.W. 1991. Characteristics and function of large woody debris in streams draining old-growth, clear-cut and second-growth forests in southwestern Washington. Can. J. Fish. Aquat. Sci. **48**: 2499–2508.

Bird, G.A., and Kaushik, N.K. 1983. Coarse particulate matter in streams. *In* Perspectives in running water ecology. *Edited by* M.A. Lock. Plenum Press, New York.

Bisson, P.A., Bilby, R.E., Bryant, M.D., Dolloff, C.A., Grette, G.B., House, R.A., Murphy, M.L., Koski, K.V., and Seddell, J.P. 1987. Large woody debris in forested streams in the Pacific Northwest: past, present, and future. *In* Streamside management: forestry and fishery interactions. *Edited by* E.O. Salo and T.W. Cundy. University of Washington Press, Seattle, Wash.

Brown, L.R., Moyle, P.B., and Yoshiyama, R.M. 1994. Historical decline and current status of coho salmon in California. N. Am. J. Fish. Manage. **14**: 237–261.

Bryant, M.D. 1985. Changes thirty years after logging in large woody debris, and its use by salmonids. *In* Riparian ecosystems and their management: reconciling conflicting uses. *Edited by* R.R. Johnson, C.D. Ziebell, D.R. Patton, P.F. Folliott, and R.H. Hamre. U.S. For. Serv. Gen. Tech. Rep. RM-120.

Conover, W.J. 1980. Practical nonparametric statistics. 2nd ed. John Wiley & Sons, New York.

Dolloff, C.D. 1986. Effects of stream cleaning on juvenile coho salmon and Dolly Varden in southeast Alaska. Trans. Am. Fish. Soc. **115**: 743–755.

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Emmingham, B., and Hibbs, D. 1996. Riparian area silviculture in western Oregon: research results and perspectives. COPE (Coastal Oregon Productivity and Enhancement), **10**: 24–27.

Frissell, C.A. 1992. Cumulative effects of land use on salmon habitat in Southwest Oregon coastal streams. Ph.D. thesis, Oregon State University, Corvallis, Oreg.

Grette, G.B. 1985. The role of large organic debris in juvenile salmonid rearing habitat in small streams. M.S. thesis, University of Washington, Seattle, Wash.

Hartman, G.F., and Scrivener, J.C. 1990. Impacts of forestry practices on a coastal stream ecosystem, Carnation Creek, British Columbia. Can. Bull. Fish. Aquat. Sci. No. 223.

Heimann, D.C. 1988. Recruitment trends and physical characteristics of coarse woody debris in Oregon Coast Range streams. M.S. thesis, Oregon State University, Corvallis, Oreg.

Hicks, B.J., Hall, J.D., Bisson, P.A., and Sedell, J.R. 1991. Responses on salmonids to habitat changes. *In* Influences of forest and rangeland management on salmonid fishes and their habitats. *Edited by* W.R. Meehan. Am. Fish. Soc. Spec. Publ. No. 19.

Keller, E.A., and Swanson, F.J. 1979. Effects of large organic debris material on channel form and fluvial processes. Earth Surf. Processes, **4**: 361–380.

Leopold, L.B., Wolman, M.G., and Miller, J.P. 1964. Fluvial processes in geomorphololgy. W.H. Freeman and Co., San Francisco, Calif.

Milliken, G.A., and Johnson, D.E. 1992. Analysis of messy data. Vol. I: Designed experiments. Chapman and Hall, New York.

Montgomery, D.R, Buffington, J.M., Smith, R.D., Schmidt, K.M., and Pess, G. 1995. Pool spacing in forest channels. Water Resour. Res. **31**: 1097–1105.

Montgomery, D.R., Abbe, T.B., Buffington, J.M., Peterson, N.P., Schmidt, K.M., and Stock, J.D. 1996. Distribution of bedrock and alluvial channels in forested mountain drainage basins. Nature (Lond.), **381**: 587–588.

Murphy, M.L., and Koski, K.V. 1989. Input and depletion of woody debris in Alaska streams and implications for streamside management. N. Am. J. Fish. Manage. **9**: 427–436.

Murphy, M.L., Heifetz, J., Johnson, S.W., Koski, K.V., and Thedinga, J.F. 1986. Effects of clear-cut logging with and without buffer strips on juvenile salmonids in Alaskan streams. Can. J. Fish. Aquat. Sci. **43**: 1521–1533.

Pentec Environmental. 1996. Hoko basin watershed analysis. Resource assessment and prescription report. Wash. Department of Natural Resources, Olympia, Wash.

Ralph, S.C., Poole, G.C., Conquest, L.L., and Naiman, R.J. 1994. Stream morphology and woody debris in logged and unlogged basins of western Washington. Can. J. Fish. Aquat. Sci. **51**: 37–51.

Reeves, G.H., Everest, F.H., and Nickelson, T.E. 1988. Identification of physical habitats limiting the production of coho salmon in western Oregon and Washington. U.S. For. Serv. Gen. Tech. Rep. PNW-GTR-245.

Smith, R.D., Sidle, R.C., Porter, P.E., and Noel, J.R. 1983. Effects of experimental removal of woody debris on the channel morphology of a forest, gravel-bed stream. J. Hydrol. **152**: 153–178.

Swanson, F.J., and Lienkaemper, G.W. 1978. Physical consequences of large organic debris in Pacific Northwest streams. U.S. For. Serv. Gen. Tech. Rep. PNW-GTR-60.

Tabor, R.W., and Cady, W.M. 1978. Geologic map of the Olympic Peninsula. U.S. Geol. Surv. Misc. Invest. Ser. Map I-993.

Triska, F.J., Sedell, J.R., and Gregory, S.V. 1982. Coniferous forest streams. *In* Analysis of coniferous forest ecosystems in the western United States. *Edited by* R.L. Edmonds. Hutchinson-Ross Publishing Co., Stoudsburg, Pa.

Veldhuisen, C.N. 1990. Coarse woody debris in streams of Drift Creek Basin, Oregon. M.S. thesis, Oregon State University, Corvallis, Oreg.

Washington Department of Fish and Wildlife and Northwest Indian Treaty Tribes. 1994. Salmon and steelhead stock inventory. Washington Department of Fish and Wildlife, Olympia, Wash.

Washington Forest Practices Board. 1995. Standard methodology for conducting watershed analysis. Version 3. Washington Forest Practices Board, Olympia, Wash.

Appendix

LWD volumes and piece counts for old-growth derived (OG) and second-growth derived (SG) LWD by stream site in 1982 and 1993.

Stream	Stream No.	Logging-history group	1982 Volume (m^3) OG	1982 Volume (m^3) SG	1982 Pieces OG	1982 Pieces SG	1993 Volume (m^3) OG	1993 Volume (m^3) SG	1993 Pieces OG	1993 Pieces SG
Cold	1	LOG	91.06	0.00	82	0	35.39	12.82	29	34
E.B. Middle Dickey	2	LOG	37.53	0.00	37	0	1.94	9.79	6	18
Elk (Calawah)	3	LOG	74.35	0.00	48	0	15.45	12.85	17	30
Falls	4	LOG	65.52	0.00	82	0	30.89	10.37	26	34
Mima Smith	5	LOG	75.55	0.00	53	0	59.57	17.58	36	57
Mosquito	6	LOG	74.11	0.00	84	0	24.43	11.69	17	34
Snahapish	7	LOG	100.25	0.00	56	0	50.16	0.00	63	0
Elk (Hoh)	8	YSG	47.33	1.93	22	10	19.84	15.88	2	25
Goodman	9	YSG	59.52	2.44	53	19	30.12	7.16	33	44
Hoko	10	YSG	10.87	2.45	11	5	5.74	3.19	4	16
Kalaloch	11	YSG	53.72	1.41	42	16	21.84	6.32	29	38
Mill	12	YSG	14.24	4.59	21	26	26.90	8.87	22	71
Mosquito (Ex)	13	YSG	56.98	0.43	52	7	5.87	14.72	3	46
Sand	14	YSG	41.65	1.21	50	9	3.41	15.10	2	44
Bear (Hoh)	15	MASG	12.89	0.25	13	1	3.77	1.91	6	7
Bear (Soleduck)	16	MASG	51.57	2.05	22	12	37.46	7.35	16	20
Cub	17	MASG	67.16	3.92	30	13	45.95	4.86	18	16
E.F. Dickey	18	MASG	37.80	3.01	41	23	7.02	11.58	11	51

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Appendix (*concluded*).

Stream	Stream No.	Logging-history group	1982 Volume (m^3) OG	1982 Volume (m^3) SG	1982 Pieces OG	1982 Pieces SG	1993 Volume (m^3) OG	1993 Volume (m^3) SG	1993 Pieces OG	1993 Pieces SG
Elk (Queets)	19	MASG	14.24	2.25	31	19	12.72	4.02	22	18
Ellis	20	MASG	31.81	1.05	16	12	11.73	2.93	3	20
Gunderson	21	MASG	13.39	1.67	24	12	14.74	2.22	18	17
Bockman	22	OSG	48.66	16.30	20	58	26.65	16.41	8	43
Braden	23	OSG	28.64	3.13	14	14	20.20	10.77	5	38
Charley	24	OSG	74.46	15.52	40	52	76.21	20.50	19	30
Green	25	OSG	7.53	6.48	11	26	20.27	12.22	8	26
Lake	26	OSG	47.78	7.63	35	18	26.24	13.63	22	30
Shuwah	27	OSG	53.06	22.01	31	22	53.40	39.00	38	93
Tassel	28	OSG	53.77	1.58	10	10	78.26	11.10	7	26

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Estimating the value of in-season estimates of abundance of sockeye salmon (*Oncorhynchus nerka*)

Michael R. Link and Randall M. Peterman

Abstract: Fishwheels have recently replaced a gillnet test fishery for in-season estimation of escapement of sockeye salmon (*Oncorhynchus nerka*) to the Nass River, British Columbia. We used an empirically based Monte Carlo simulation model to estimate the potential benefits (in terms of future harvests) of using this new method. We found that using the information from the fishwheels in place of the gillnet test fishery may increase the average annual catch from current ocean fisheries by 2.7% ($229 000) due to the greater accuracy of in-season estimates. When the additional costs of operating the fishwheels instead of the gillnet test fishery were taken into account, the fishwheel program still resulted in an annual net benefit of about $180 000. Eliminating the deviations from the target escapement for Nass River sockeye salmon by having perfect monitoring of escapement and perfect control over harvesting has a potential annual value of more than $1 million (CAN). However, much greater benefits from fishwheels are unlikely to be realized because of the highly variable response of the commercial fishing fleet to additional fishing opportunities and the 5-day lag of the escapement estimates provided by fishwheels.

Résumé : Dernièrement, on a remplacé par des tourniquets une pêche d'essai au filet maillant pour l'évaluation au cours de la saison de l'échappée de saumon rouge (*Oncorhynchus nerka*) vers la Nass (Colombie-Britannique). Nous avons utilisé un modèle de simulation de Monte Carlo fondé sur des données empiriques afin d'évaluer les avantages (en fonction de captures futures) que pourrait avoir cette nouvelle méthode. Nous avons constaté que les données fournies par les tourniquets, qui remplacent la pêche d'essai au filet maillant, peuvent augmenter les captures annuelles moyennes des pêches maritimes actuelles de 2,7 % (229 000 $) en raison de la plus grande précision des évaluations pendant la saison. Lorsque les coûts supplémentaires d'exploitation des tourniquets ont été pris en compte, le programme des tourniquets s'est quand même traduit par un bénéfice annuel net d'environ 180 000 $. L'élimination des écarts de l'échappée par rapport à la cible établie pour le saumon rouge de la Nass grâce à une surveillance parfaite de l'échappée et à un contrôle excellent sur les captures a une valeur annuelle potentielle de plus de 1 million de dollars (CAN). Toutefois, il n'est guère probable que les tourniquets permettent de réaliser des bénéfices beaucoup plus importants à cause de la très grande variabilité de la réponse de la flottille de pêche commerciale à de nouvelles possibilités de pêche et du délai de 5 jours pour obtenir les évaluations de l'échappée calculées grâce à ces dispositifs.
[Traduit par la Rédaction]

Introduction

Acquiring better information about the status of fish stocks is clearly beneficial. However, because funding for such stock assessment programs is limited, fisheries managers must carefully allocate funds among various programs for gathering data. To do so, the benefits of better data should be explicitly compared with the costs of acquiring that information. However, this comparison is rarely done in fisheries (and in most other natural resource fields) because the benefits of stock assessment are difficult to quantify. This is also true of Pacific salmon (*Oncorhynchus* spp.) fisheries, where managers must choose among several methods to assess the in-season abundance of returning fish.

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Pacific salmon fisheries are typically managed to meet escapement goals that are believed to produce the optimal long-term harvest from the spawning population (Ricker 1975; Wright 1981). Managers try to achieve this target escapement by regulating, among other things, the time and place where fishing vessels operate (Minard and Meacham 1987; Sprout and Kadowaki 1987). These regulations are usually set weekly or daily within a season and are based on several types of data: escapement to date, the historical timing of the returning fish stock, and the expected amount and efficiency of the fishing gear. However, meeting the target escapement is often difficult because of large variability in (*i*) the annual abundance of returning fish, (*ii*) the timing of the run (i.e., early, average, or late), (*iii*) migration routes used by the fish moving through the fishing area, (*iv*) the amount of fishing gear present, and (*v*) estimates of the catch and escapement made during the season. Several authors have developed various quantitative methods to help managers meet the target escapement by accounting for variation in these factors (Paulik and Greenough 1966; Walters and Buckingham 1975; Lord 1976; Henderson et al. 1987; Minard and Meacham 1987; Sprout and Kadowaki 1987; Fried and Hilborn 1988; Noakes 1989). However, even with elaborate quantitative techniques, managers cannot completely account for these sources of variation, as is indicated

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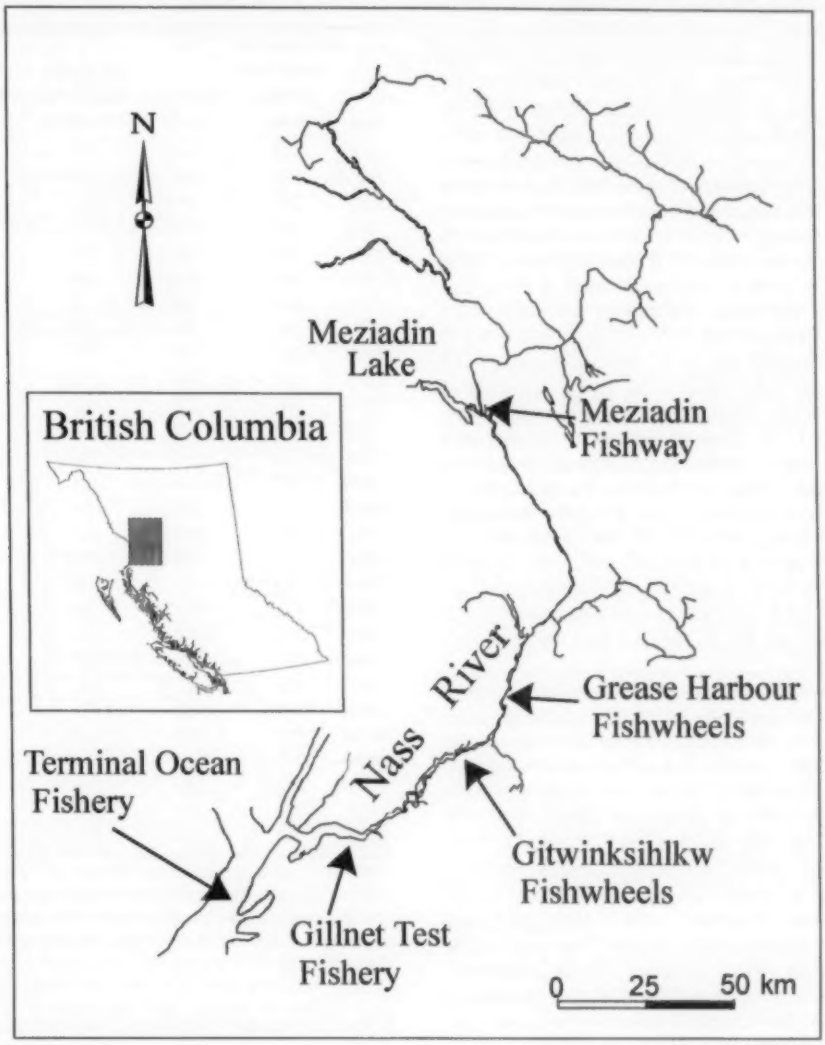
Fig. 1. Locations of the terminal commercial fishing area (area 3-12) and escapement monitoring sites on the Nass River.



by the wide frequency distribution of actual escapements around targets typically found in intensively managed salmon fisheries (Bocking and Peterman 1988; Eggers 1992). This observation raises the following general question: should more time and money be spent improving data for the in-season management of salmon?

Some authors have advocated improving in-season escapement estimates of salmon (e.g., Pearse 1982). For instance, by using a quantitative model, Lord (1976) found that increasing the precision of in-season forecasts of the abundance of salmon recruits decreased deviations from the escapement goal and increased mean catch, but he did not determine the costs associated with increasing the precision of in-season forecasts of abundance. Similarly, Eggers (1993) found that a constant escapement policy coupled with improved monitoring would outperform other policies. However, he also did not examine the costs of improved information.

We examined this type of information problem, while taking costs into account, on the Nass River, British Columbia, where managers have used two different methods of estimating the abundance of returning sockeye salmon (*Oncorhynchus nerka*) during the season. A standardized gillnet test fishery was used on the Nass River from 1963 to 1993 to estimate the daily escapement of sockeye salmon upstream past the commercial fishing area, and this information was used to manage a terminal commercial net fishery (area 3-12, Fig. 1; Southgate et al. 1990). Fishing effort in area 3-12 was managed to attempt to meet the constant annual escapement target of 200 000 fish normally used by managers. However, due to the factors described above, the actual spawning escapement has varied from 91 000 to 660 000 (Table 1; Cox-Rogers and Jantz 1993). In 1994, the gillnet test fishery was replaced with a fishwheel test fishery (Fig. 1; Meehan 1961; Donaldson and Cramer 1971; Link and English 1996; Link et al. 1996).

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Although the fishwheels have improved the accuracy and precision of in-season escapement estimates for the Nass River sockeye salmon stock (Link and English 1996), there are several reasons to believe that their better information may result in very little net benefit (where net benefit is defined as the additional dollar value of the commercial harvest resulting from using the fishwheel monitoring method minus the additional cost of using the fishwheels to obtain in-season estimates of abundance). First, the annual cost of the fishwheel program is almost 70% greater than the gillnet test fishery. Second, because of the morphology of the river channel, the fishwheels must be located near the village of Gitwinksihlkw, about 3–7 days of travel for sockeye salmon upstream of the gillnet test fishery (Fig. 1). This delay in obtaining abundance estimates means that managers are less able to quickly adjust openings of the commercial fishery in response to unexpected changes in abundance. Third, most of the Nass River sockeye salmon are intercepted by fisheries outside the Nass River terminal fishing area 3-12. In those outside areas, management objectives focus on other nearby stocks such as the Skeena River sockeye, which makes it difficult for managers to achieve optimal escapements to the Nass River by manipulating harvesting effort in area 3-12. Fourth, the fishing effort in the terminal fishing area 3-12 for Nass River sockeye is highly variable from week to week, depending on fishing opportunities elsewhere. Thus, even with better information available, it may be difficult to achieve the escapement goal with fluctuating fishing effort.

Our research was designed to determine whether the additional benefits (greater harvests) of the fishwheel program would be greater than its additional cost (cost above that of the gillnet test fishery). This question cannot be answered by simply comparing harvests in the few years when fishwheels have been used with those when the gillnet test fishery was used because (aside from the very small sample of years for fishwheels and no time yet for feedback between fish generations) many conditions such as abundances have changed and would confound interpretations. Therefore, a model is needed where different monitoring methods can be simulated and where their expected benefits can be estimated. This will permit determining whether the added value of a data gathering program is expected to be greater than its added costs.

Therefore, unlike most similar studies, we used a Monte Carlo simulation model that included not only the dynamics of the fish population, but also management decision making, fishing fleet dynamics, and economic information. The model explicitly took into account uncertainties in variables such as fish abundance, run timing, fishing effort, and efficiency of fishing gear. Our analysis focused on comparing the two methods of making *in-season* estimates of escapement upstream past the commercial fishing area; we did not incorporate the annual estimates of spawners at the Meziadin fishway because that information arrives too late to be useful. Thus, unless indicated otherwise, references to escapement estimates here refer to the in-season estimates derived from either the gillnet test fishery or fishwheel escapement monitoring programs.

Methods

Data sources

We obtained annual commercial catch data for Nass River sockeye salmon for the period 1966–1992 and daily catch and effort data for statistical area 3-12 for the period 1982–1992 from K. English (LGL Ltd., Sidney, B.C., personal communication). We obtained estimates of the annual Nisga'a food fishery catch from Nisga'a Tribal Council data reports. Daily and annual cumulative indices for the gillnet test fishery for the years 1964–1993 came from L. Jantz (Department of Fisheries and Oceans, Prince Rupert, B.C., personal communication). Estimates of daily and total annual sockeye abundance at the Meziadin River fishway (Fig. 1), the portion of escapement bound for Meziadin, and the age composition of the annual run were obtained from L. Jantz (personal communication). Historical estimates of the annual abundance of sockeye spawners for the Nass River have been considered very reliable and measured with relatively little error compared with many other salmon stocks on the Pacific coast. This is because a large portion (average 77%, range 45–94%) of the run is visually counted at the Meziadin River fishway each year (Link and English 1996).

Table 1. Historical performance of the gillnet test fishery on the Nass River, 1966–1993.

Year	Cumulative annual test fishing index	Expansion factor	Predicted escapement (thousands)	Actual escapement (thousands)	% error in predicted escapement
1966	182	500	91	127	–29
1967	191	500	95	98	–3
1968	265	500	133	117	13
1969	253	500	127	201	–37
1970	288	400	115	137	–16
1971	363	400	145	272	–47
1972	235	400	94	198	–53
1973	489	538	263	312	–16
1974	320	549	176	217	–19
1975	216	550	119	91	30
1976	304	550	167	166	0
1977	466	550	256	427	–40
1978	270	550	148	170	–13
1979	285	641	182	236	–23
1980	253	600	152	177	–14
1981	387	671	260	281	–8
1982	427	610	260	333	–22
1983	285	613	175	204	–14
1984	322	616	198	208	–5
1985	416	612	255	390	–35
1986	280	650	182	218	–17
1987	228	661	151	212	–29
1988	259	700	181	157	15
1989	274	675	185	133	39
1990	247	625	154	173	–11
1991	353	650	230	319	–28
1992	414	650	269	660	–59
1993	330	783	259	487	–47

Note: The expansion factor was the value of $1/q$ (q is the catchability coefficient) used in-season to predict the escapement from the test index. The actual escapement was derived as the estimated total escapement (based on counts at an upstream fishway) plus the estimated Nisga'a harvest above the test fishery.

Simulation model

A generalized flowchart of the stochastic simulation model (Fig. 2) indicates its major components, which are described in detail below. First, the model calculated the population dynamics of the sockeye

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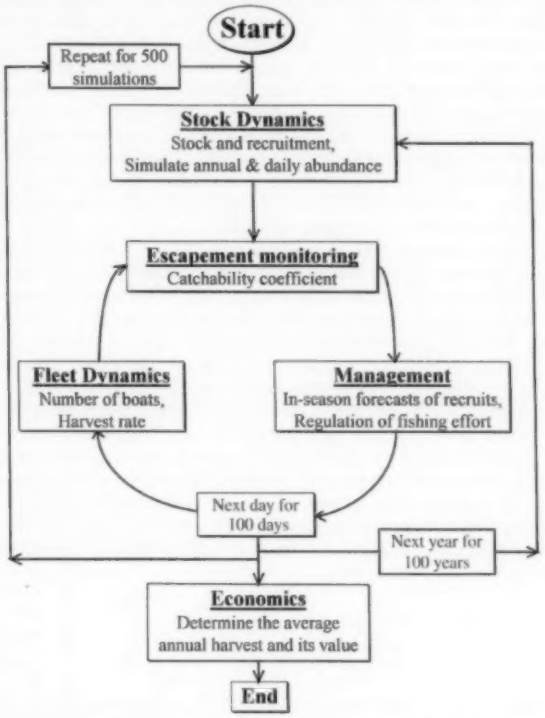
Fig. 2. Generalized flowchart of the in-season simulation model used to evaluate the benefits of improvements to the sockeye salmon escapement estimates on the Nass River.



stock, taking into account the stock–recruitment relationship and the interception of Nass River bound recruits in outside fisheries. Next, the remaining fish entered the terminal fishing area 3-12 and were subject to harvest by the commercial fishing fleet. The model then simulated the monitoring of fish escaping past area 3-12, which fed estimates of abundance into the in-season management algorithm, which in turn affected the commercial harvesting. Nass River sockeye salmon were also harvested in the river by a "food fishery" conducted by the Nisga'a people. Unharvested fish escaped to spawn. Each simulation was 100 years long and was repeated 500 times under each type of escapement monitoring. We first determined the expected, or weighted average, forecast of yield from the fishery using a simulated gillnet test fishery to provide in-season estimates of the escapement. We then repeated the same calculations, but instead used fishwheels as the test fishing method. From the results, we estimated the additional value of the catch and additional costs from using the fishwheels instead of the gillnet test fishery. Details of these various components follow.

Stock dynamics

Stock and recruitment: First, we used a Ricker stock–recruitment function (Ricker 1975) with a lognormal error term (Peterman 1981) to simulate the total recruits (R, numbers of fish) from annual numbers of spawners (S):

$$(1) \qquad R = Se^{a(1 - S/b) + v}$$

where a is a productivity parameter, b is the equilibrium stock abundance in the absence of harvest, and v is a normally distributed random error term with variance σ_v^2. The parameters were estimated by least squares regression of the natural logarithm of R/S on S using annual catch and escapement data for the brood years 1966–1988 ($a = 1.79$, $b = 508\,762$ fish, $\sigma_v = 0.485$), and the escapement target, or $S_{Optimum} = 198\,680$ fish, was estimated by iterative search. We apportioned recruits from each brood year among ages according to the average proportional distribution by age for the years 1966–1992. The model used the simulated escapement derived from modeling the dynamics of the fish stock, the fishing fleet, and the management actions. The model used the escapement target (200 000 fish) to calculate the number of recruits for the first 6 years because there was no simulated escapement for these initial years. By using a stock–recruitment function, the model output reflected the feedback effect of management decisions and fleet and stock dynamics on the mean annual harvest caused by both underescapement and overescapement.

Simulation of annual and daily abundance: This stochastic component of the model provided a representative time series of daily abundance in the simulated area 3-12 fishery and the Nass River test fishing locations. It was not necessary to exactly mimic any particular year's historical run; rather, we generated a representative range of total annual abundance and temporal patterns of the run timing based on historical patterns, as follows.

To model the relationship between the harvest rate in the fisheries *outside* area 3-12 and the abundance of recruits, we used a linear regression of the proportional harvest rate on total recruits to reach area 3-12 for the period 1982–1992 ($Y = 0.65 - 0.00028X$, $n = 11$, $r^2 = 0.59$, $P = 0.054$). We used this regression model with a normally distributed error term ($\sigma = 0.1$) to model this component stochastically to provide representative variation in the number of fish returning to area 3-12. To simulate a time series of daily sockeye salmon recruits to the area 3-12 fishery, the model randomly selected an annual run timing curve for a simulated year from the historical S-shaped run timing curves (cumulative abundance as a function of date) and multiplied the simulated annual abundance of recruits by the daily proportion derived from the run timing curve. The historical run timing curves were based on the daily portion of the annual total gillnet test fishery index for the years 1967–1993. The simulated daily abundance was then moved through the fishery and test fishery locations according to travel times determined from tagging studies (Link 1995). We used values of 2 days for the travel time through area 3-12 and 5 days from the gillnet test fishing site to the fishwheels (Fig. 1).

Fleet dynamics

To calculate the harvest rate of fish *inside* area 3-12, we determined the number of fishing vessels present and the resulting harvest rate on a given day when the commercial fishery was open in the model. It has been observed previously that the number of fishing vessels attracted to fish in an area is positively related to various indices of abundance of salmon (Hilborn 1985). Therefore, to describe this numerical response of the number of boats ("Boats") to changes in daily number of sockeye salmon in area 3-12 ("fish"), we used a descriptive, flexible function with a lognormal error term:

$$(2) \qquad \text{Boats} = \alpha_1(\text{fish})^{\beta_1 + v_1}$$

where α_1 and β_1 were estimated with linear regression of $\log_e$(Boats) on $\log_e$(fish). We tested whether there was significant nonlinearity in the form of eq. 2 by using a null hypothesis, H_0: $\beta_1 = 1$. Although there was considerable noise in the data ($r^2 = 0.2$, $\sigma_v = 0.96$), the regression was significantly nonlinear ($\log_e(\text{Boats}) = 0.69 \cdot \log_e(\text{fish}) - 2.99$, $\alpha_1 = 0.05$, $\beta_1 = 0.69$, $n = 72$, $P = 0.0002$). The noise in the relationship was probably due to the effect of fishing opportunities on the nearby Skeena River affecting many harvesters' decisions whether to fish the Nass River. The linear model was not significant ($P = 0.18$).

Previous work has shown that the proportion of salmon harvested in a short opening is a nonlinear function of the number of fishing vessels present (Walters and Buckingham 1975). Therefore, to describe our data (Fig. 3) on the daily harvest rate of Nass River sockeye as a function of the number of fishing vessels (Boats) in area 3-12, we

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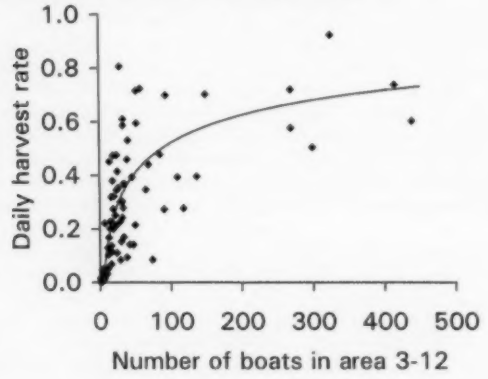
Fig. 3. Historical relationship between the number of commercial fishing vessels fishing in area 3-12 and the estimated proportional daily harvest rate of Nass River sockeye salmon.



fit the same flexible, nonlinear model as eq. 2, but used the daily number of fishing vessels as the X variable and daily proportion harvested as Y, and used data for the period 1982–1992. Regression of the transformed variates using ordinary least squares regression was significantly nonlinear ($\alpha_2 = 0.054, \beta_2 = 0.183, \sigma_{\varepsilon} = 0.2, n = 89, r^2 = 0.39$, $P(\beta_2 = 1) < 0.0001$). The simulation model used these relationships in the Monte Carlo trials, with the σ values described.

In addition, the annual Nisga'a food fishery harvest was calculated by a linear relationship between that harvest and the fish abundance, bounded by a minimum harvest rate of 25% (based on historical observations) and the maximum historical Nisga'a harvest (62 800 fish).

Management

Escapement monitoring: The in-season escapement estimates used by Nass River managers are derived assuming the standard linear relationship between catch per effort (C/f) and abundance (N):

$$(3) \qquad C/f = qN$$

where q, the catchability coefficient, is defined as the proportion of the population captured per nominal unit of fishing effort, f. The value of q used each season was based on the historical relationship between the annual escapement and the annual cumulative C/f.

We modeled the fishwheel and the gillnet escapement monitoring programs in a similar manner. At each location, a number of fish moved past the monitoring site on each day and we assumed that the measured C/f was some function of this escapement and the catchability coefficient (q) of the particular monitoring program. We also assumed that managers had an a priori estimate of q (based on historical data) that was used for the entire season to estimate the daily escapement from the C/f. As described below, we modeled the fishwheel method so that it provided unbiased estimates of the escapement with similar precision as the gillnet method whereas we modeled the gillnet method to reflect the bias that has been created by managers assuming the linear relationship of eq. 3, where $q((C/f)/N)$ was constant and independent of fish abundance.

Catchability of the gillnet test fishery: As many authors have found in other fisheries (e.g., Crecco and Savoy 1985; Winters and Wheeler 1985), the historical data for Nass River sockeye (1966–1993) suggest that the catchability coefficient of the gillnet test fishery varied inversely with the abundance of fish (Fig. 4). To test this, we fit a model previously described for this situation (Peterman and Steer 1981; Bannerot and Austin 1983):

$$(4) \qquad C/f = \alpha_3 N^{\beta_3}$$

using a linear regression of $\log_e(C/f)$ on $\log_e(N)$, where C/f was the cumulative annual test fishery index and N was the annual escapement past the gillnet test fishing site. We then tested the hypothesis that $\beta_3 = 1$ to determine whether q was density dependent. If β_3 was not significantly different from 1, then it implied that C/f was linearly related to stock abundance as in eq. 3 and thus that q was density independent and equal to α_3. However, if β_3 was significantly different from 1 and $0 < \beta_3 < 1$, then it meant that q was density dependent and highest at low abundance (Peterman and Steer 1981). In our data analysis, the null hypothesis of density-independent q was rejected ($P(\beta_3 = 1) < 0.001$), indicating that saturation of the gillnet had likely occurred at high fish abundance (Appendix). Therefore, to accurately model the functional relationship between C/f and the number of fish passing the gillnet test fishing site each day, we had to take into account the effect of fish abundance on q.

We used the annual mean and variance (CV = 25%) of q from the historical data for the modeled gillnet test fishery. To determine a daily q, the model added a daily random error to the seasonal mean q to represent daily changes in q that were unrelated to fish abundance. For this density-independent variation, we assumed a normally distributed error term with a mean of zero and a standard error based on a 15% CV (same as estimated for the fishwheels; Link 1995). To reflect the density-dependent effect of abundance of fish on the gillnet q shown above, we used Holling's (1959) "disc" equation for a type II functional response (predator consumption rate as a function of prey abundance). This predator functional response can be reformulated in fisheries terms because it is directly analogous to the relationship between catch per boat-day (C/f) of the gillnet test fishery and the number of fish passing the gillnet test fishing site on a given day (Peterman and Steer 1981):

$$(5) \qquad C/f = \frac{qN}{\left(1 + \frac{q}{(C/f)_{\max}} N\right)}$$

where N was the daily escapement and $(C/f)_{\max}$ was the maximum C/f for very large N. We assumed that the best estimate for $(C/f)_{\max}$ was the maximum daily C/f observed for the period 1963–1993 (= 42). The daily C/f from the modeled gillnet test fishery was determined by eq. 5. Equation 4 was not used to model the effect of fish on the daily q for the gillnet because its parameters were based on *annual* cumulative C/f and abundance. The test of nonlinearity of eq. 4 indicated that the season-average q over all days decreased with increasing annual escapement.

Catchability of fishwheels: We used the observed values of q from the fishwheels for the period 1992–1996 to derive estimates of the mean (0.048), interannual variability (CV = 22%), and daily variability (CV = 15%) for the fishwheel test fishery q (Link 1995). The daily measured C/f was determined by eq. 3, multiplying the daily q by the number of fish passing the site on a given day. Results from annual mark–recapture experiments have clearly shown that the estimated daily and annual catchability coefficients of the fishwheels do not vary with fish abundance.

In-season forecasts of annual recruits: We used the estimated cumulative escapement from the given test fishery, the cumulative catch in area 3-12, and the historical average run timing to forecast the annual return to area 3-12 during the simulated fishing season. The annual return to area 3-12 ($N_{3\text{-}12}$) was forecasted on a given day as the reciprocal of the historical average cumulative proportion of the run on that date ("Cumprop") multiplied by the total return to date (general method of Walters and Buckingham 1975):

$$(6) \qquad N_{3\text{-}12} = \frac{1}{\text{Cumprop}} \times (\text{cumulative escapement} + \text{cumulative 3-12 catch}).$$

The cumulative escapement to date was lagged by the appropriate travel time to each test fishing site to put it at area 3-12 on a given date.

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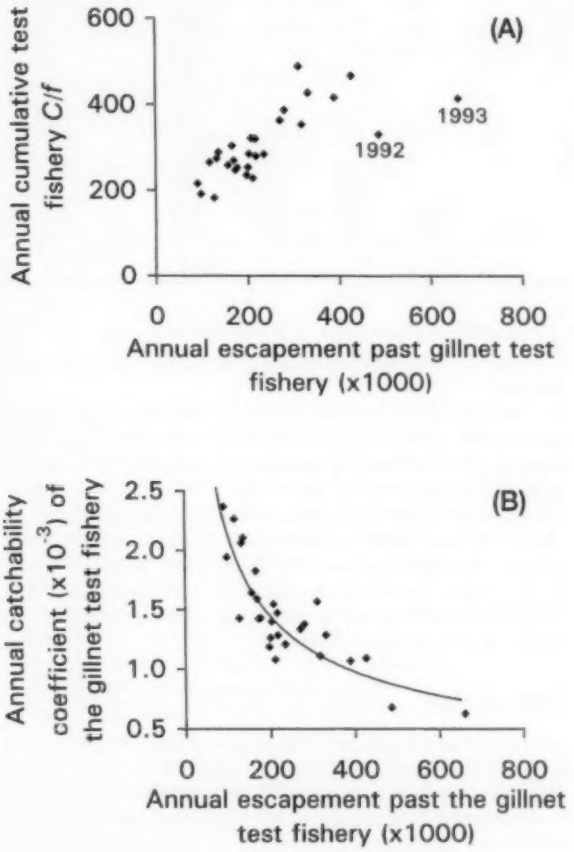
Fig. 4. (A) Historical relationship between the annual gillnet test fishing index (catch per effort, *C/f*) and the annual escapement past the test fishery (1966–1993). (B) Same as Fig. 4A except that the data are replotted as the catchability coefficient ((*C/f*)/*N*) for the gillnet test fishery.



Regulation of fishing effort: Decisions were made each week on whether to open the area 3-12 fishery the following week or, if already opened, to extend the current fishery based on the estimated number of fish remaining to be caught ("Desired catch"):

(7) Desired catch = Forecasted run – escapement target – cumulative catch

where cumulative catch is the total catch to date on the day that the calculation is made. We incorporated into the model the following decision-making procedure, which approximated the one used historically by managers (D. Peacock, Department of Fisheries and Oceans, Prince Rupert, B.C., personal communication). First, on the sixth day of the week (Friday), if the desired catch was greater than zero, the fishery was opened for 1 day on the first day of the following week. Then, after the initial 1-day opening, the catch and escapement data were used to produce a new estimate of the desired catch. If the desired catch was greater than zero on this day, the fishery was extended 1 day. This process was repeated each day up to a maximum of 3 consecutive days of fishing per week in June and a maximum of 5 consecutive days for the remainder of the season. Second, if there was no fishery on the first day of the week, we assumed that managers reviewed the escapement information on the third day of the week and if the desired catch was greater than zero, a fishery was held on day 4. The decision to extend this late-week fishery 1 day was made in the same manner as described above for the early-week fishery. In all situations, we assumed that no fishing occurred on days 6 and 7.

The run timing for the Nass River sockeye can be very contracted (most fish arriving during only a few weeks) and the commercial fishery can miss large portions of the run when this happens. Therefore, managers have chosen to fish some days in July, even if the desired catch is not greater than zero, to get additional information on abundance (using the commercial catch to include in the forecast of the total run) and to allow time to exert an adequate harvest rate if the run is contracted. This is usually done as long as there are no serious conservation concerns that the escapement is well below target. Therefore, we assumed that the fishery would open a minimum of 1 day per week for the last 3 weeks of July, as long as the forecasted spawning escapement on the previous Friday did not fall below 150 000 fish (D. Peacock, personal communication).

Economic valuation

To estimate the net economic value of each Nass River sockeye salmon caught in all fisheries, we used the British Columbia coastwide average wholesale value (1993 CAN$) for the period 1990–1991 minus harvesting and processing costs (R. Mylchreest, Department of Fisheries and Oceans, Vancouver, B.C., personal communication). This method approximates the benefit of small incremental increases or decreases to the British Columbia salmon catch. Using an average weight of 2.9 kg per fish for Nass River sockeye salmon, we estimated the net value of one Nass River sockeye to be $20.79 (Link 1995).

The annual costs associated with each escapement monitoring technique are well known: about $72 500 for the gillnet test fishery and $121 500 for the fishwheel test fishery (Link 1995). Thus, since the fishwheel program costs $49 000 more than the gillnet test fishery, its use would be justified (based on catches from the fisheries) if it increased the average annual harvest by more than 2357 sockeye ($49 000/$20.79).

Simulations with these model components were done separately for the gillnet and fishwheel test fisheries.

Results

Simulation results indicated that using the fishwheel program instead of the gillnet test fishery increased the expected annual yield from the sockeye stock by 11 000 fish (2.7%), worth an additional $229 000 (Table 2). By subtracting the additional cost of the fishwheel program ($49 000), we estimated its net value to be $180 000 per year (Fig. 5). The simulated fishwheel program decreased the average escapement from 246 000 to 234 000 fish (4.9%) and increased the area 3-12 landings from 88 000 to 102 000 fish (16%) compared with managing using the gillnet test fishery (Table 2). The harvest from fisheries outside area 3-12 and from the Nisga'a food fishery decreased slightly (Table 2). Using the fishwheels increased the number of days the fishery was open by 30% (from 13 to 17 days annually) and annual fishing effort by 23% (from 493 to 605 boat-days) (Table 2).

Value of perfect monitoring and perfect harvesting

To estimate an upper limit for the expected value of monitoring the escapement, we ran a series of simulations where the escapement was known exactly on each day in the model (perfect monitoring). We then compared the yield under these situations with the baseline results for the gillnet test fishery. We estimated the benefits of perfect monitoring over the baseline

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Table 2. Mean annual results from Monte Carlo simulations of the Nass River sockeye fishery and test fisheries.

	Thousands of fish									
				Catch by area						
	Total recruits	Escapement	Total catch	Outside area 3-12	Area 3-12	Nisga'a	No. of days fishing	Total effort (boat-days)	Value of catch (×$1000)	Incremental increase in value over the baseline gillnet scenario (×$1000)
Historical data	581	225	356	269	54	33	17	388	7401	
Simulation results										
Baseline										
Gillnet method	656	246	410	288	88	34	13	493	8524	
Fishwheel method	655	234	421	286	102	33	17	605	8753	229
Perfect monitoring										
At the gillnet site	644	215	429				18	625	8919	395
At the fishwheel site	652	230	422				17	618	8773	249
Perfect harvest ability	634	174	460	—	—	—	—	—	9563	1040

Note: Values are from 500 simulations of 100 years duration.

gillnet scenario to be $395 000 per year if that perfect information were gathered at the site of the gillnet test fishery, but only $249 000 per year if it came from the fishwheel site (5 days of further travel upstream for sockeye). Therefore, perfect monitoring at the gillnet site can be expected to be worth $146 000 more than perfect monitoring at the fishwheel site because of the more timely nature of the gillnet escapement information.

These results refer to the case where managers have the ability to know the daily escapement without error but where the commercial fishery still has variability associated with it. We wished to determine the relative importance of this lack of complete control over fishing to the lack of perfect escapement monitoring. Thus, in other simulations, we assumed that managers were able to perfectly control the harvesting to achieve the target escapement. To determine the value of this situation, we ran simulations where all fish that entered area 3-12 in excess of the escapement target were harvested each year. Under this scenario of perfect control of harvest, the value of the yield increased $1 040 000 annually over the baseline gillnet test fishery scenario (Table 2).

Sensitivity analysis

To examine the sensitivity of our conclusions to the assumed parameter values, we varied each parameter between ±50% of their baseline values and compared the yield with that from the baseline scenario for each of the two types of test fisheries, gillnet and fishwheels. The conclusion that the fishwheel program had a positive net dollar value was insensitive to all changes in the parameters. The net value of the fishwheels fell below $100 000 in only two situations: (*i*) when we assumed that $(Clf)_{max}$ (eq. 5) was equal to 63 (i.e., less saturation effect than used for the baseline, net value = $63 000, Fig. 5) and (*ii*) when we assumed that the travel time between the gillnet site and the fishwheel site was 8 days instead of the baseline value of 5 days ($62 000, Fig. 6). The net value of the fishwheel technique was sensitive to the assumed travel time between the two monitoring sites, although the differences did not affect our general conclusions that the net benefit was greater than zero (Fig. 6). With the exception of assuming greater saturation effect of the gillnet than the baseline case (Fig. 5), all other sensitivity analyses indicated that the net value of the fishwheels never exceeded $300 000 annually (i.e., for 1 day of travel time from the gillnet site to the fishwheels).

The increase in yield from using the fishwheel test fishery was derived from the improved accuracy of the fishwheels because, for the baseline simulation, we assumed a similar precision in escapement estimates for the gillnet and fishwheels whereas we assumed that actual q changed with abundance for the gillnet method alone, leading to inaccuracy because managers assumed that the gillnet q was not affected by abundance. Increasing the precision of either technique (CV of q to 0%) had little effect on our quantitative results and no effect on our general conclusions.

Discussion

Based on our results, the fishwheel escapement monitoring program is expected to increase the value of annual catches of Nass River sockeye salmon by $229 000 above the catches that would result from using the gillnet test fishery monitoring program. This increase in dollar value of harvests is due to the greater accuracy of abundance estimates, and this additional benefit is $180 000 per year greater than the additional cost of using fishwheels instead of the gillnet test fishery. Thus, there is a net benefit expected from changing the method of in-season monitoring of Nass River sockeye to fishwheels, despite the difficult management situation created by the large portion of total Nass River sockeye catch (average of 86%, range of 61–100%, 1982–1992) that is harvested in mixed-stock fisheries outside area 3-12.

In a study of the Skeena River, Steer (1988) also found that improving escapement estimates would produce a net benefit. However, in that case, Steer (1988) compared using the commercial catch-per-effort data with using a standardized gillnet test fishery to monitor the abundance of sockeye salmon. He found via an empirically based simulation model that the standardized gillnet test fishery reduced expected deviations from the optimum escapement. The resulting increase in dollar yield from the commercial catch was estimated to be greater than the cost of the gillnet test fishery. In contrast with our study, he used a once-weekly decision-making process, which tends to mask important within-week decision making typically used in managing salmon fisheries. In a study of sockeye

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Fig. 5. Sensitivity of the net annual value of the fishwheel technique to the assumed value of the maximum *C/f* value for the gillnet test fishery, the $(C/f)_{max}$ parameter in eq. 5.

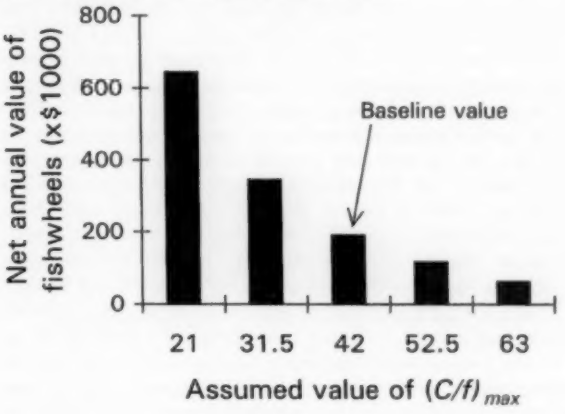
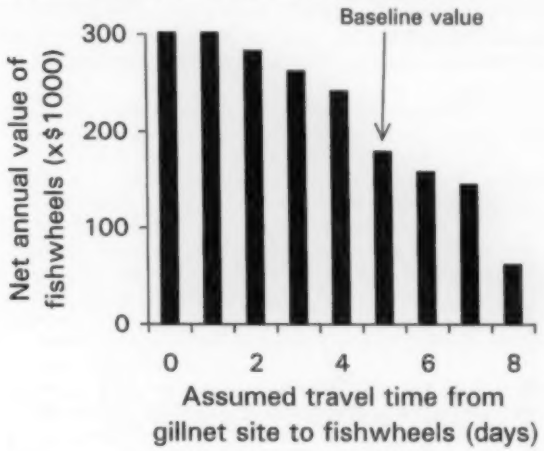


Fig. 6. Sensitivity of the net annual value of the fishwheel technique to the assumed time for sockeye salmon to travel from the gillnet test fishery site to the fishwheel monitoring site.



salmon in Bristol Bay, Alaska, Eggers (1992) estimated the benefits of decreasing the errors in meeting target escapement (in part through better in-season abundance data). Eggers (1992) found that the ratio of benefits (increased dollar value of harvest) to the incremental cost of management was 10:1. However, unlike our study, he did not determine the benefits of managing the fishery without the additional information provided by the existing in-season estimation program. Most significantly, Eggers (1992) may have overestimated the benefits by incorrectly attributing some of them to management; he did not remove the portion of recent increases in abundance that resulted from improved oceanographic conditions (Francis and Hare 1994; Adkison et al. 1996).

The dynamics and logistics of the commercial fishing fleet in area 3-12 will hinder attaining further benefits from better escapement information beyond the $180 000 per year. One reason is that, while the fishwheel escapement information is more accurate than estimates from the gillnet test fishery, because estimates from fishwheels are delayed 5 days, the decisions to open or close the fishery come later, on average, than under similar gillnet information, and therefore, there are fewer fish left to pass through the ocean fishing area that year. As a result, the total effort (boat-days) using the fishwheels was only 23% greater than when using the gill nets, even though there were 31% more days of fishing. This discrepancy occurred because the response of the commercial fleet is a function of the abundance of fish; more openings will not always result in substantially more effort, and openings that occur late when the abundance has diminished tend to attract fewer boats.

Our sensitivity analyses showed that our general conclusion about the economic viability of the fishwheel escapement monitoring program was robust to various assumptions. Furthermore, we underestimated the additional value of the fishwheel escapement program for at least four reasons. Most obvious is the failure to include the benefits associated with monitoring abundance of other species of salmon. Fishwheels are superior in this regard because they capture 5–10 times as many fish as the gillnet test fishery does and therefore can be used to provide indices of abundance and biological information on these other less-abundant species of salmon. Second, we did not include the benefits of selectively harvesting fish with the fishwheels. In three of the last five years when the target escapement to the Nass River has been exceeded, a portion of the sockeye salmon catch from the fishwheels has been selectively harvested and sold on the market. Third, the relationship that we used to model the gillnet test fishery's *C/f* as a function of fish abundance did not completely account for the bias in *q* observed at historically high abundances (Fig. 7). Above about 450 000 fish escaping past the gillnet test fishery, the observed difference between the simulated and actual annual cumulative *C/f* increases (Fig. 7). The simulated saturation underestimated the actual saturation effect in the historical data because the run timing data that we used had an inherent bias. We used run timing curves derived from the gillnet test fishery data where saturation likely occurred, and this would have resulted in the data underestimating the abundance on peak days. Therefore the historical gillnet test fishery *C/f* data underestimated the daily portion of the run moving by on the peak days and in doing so provided us with "dampened" run timing curves for our model. Using these dampened curves, we could not fully model the saturation on peak abundance days. Fourth, we assumed that the Nass River sockeye salmon escapement information does not affect the management of areas outside area 3-12; historically, this was the case. However, in recent years (e.g., 1997), very low escapement to the Nass River has caused managers to regulate fisheries outside area 3-12 to protect Nass River sockeye salmon. In these situations, better escapement monitoring results in meeting the escapement target more often and creates more benefits than we have modeled. Thus, given these four reasons, the model may have overestimated benefits associated with the gillnet test fishery and consequently underestimated the added benefits of the fishwheel technique. Our general conclusion still holds, then, that the fishwheel method is the better of the two.

We have also shown that the potential benefits of improved accuracy of escapement estimates were small compared with the ability to harvest all fish that exceeded the target

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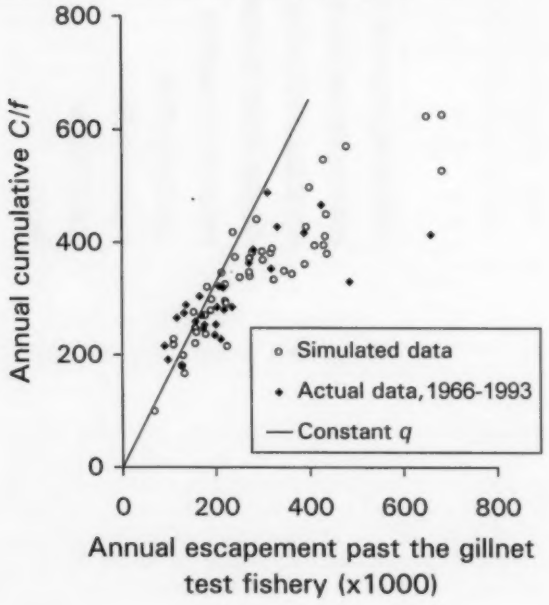
Fig. 7. Simulated and actual annual cumulative *C/f* versus escapement past the test fishery. Historical data are from the period 1966–1993; simulated data are from one stochastic run of 50 years under the assumptions of the baseline simulation of the gillnet test fishery. The constant *q* line represents the mean *q* used in the model and reflects no saturation effect and no stochastic variation.



escapement. Perfect monitoring of the escapement increased the annual yield by $395 000 whereas the ability to perfectly harvest all excess fish increased the annual yield by $1 040 000. Walters and Buckingham (1975) similarly found in a study of the Skeena River sockeye salmon that the harvest dynamics of the commercial fishing fleet have far more influence on the performance of an in-season control system than does better information on the abundance of recruits. They found that even with perfect preseason forecasts of the abundance of recruits, there were still large errors in meeting the catch and escapement objectives. These errors were largely due to an inability to predict the response of the fishing fleet (number of vessels to expect) and its subsequent weekly harvest rate. However, the control system of Walters and Buckingham (1975) assumed that decisions regarding the duration of fishing openings were made weekly; once they were set at the start of the week, the length of the opening did not change midweek. This is different from the control system in our model where decisions could be made daily to extend the fishery if the catch objective was not met or to close the fishery if it was met. Therefore, the decision-making routine used in our model allowed for more realistic and precise control over the fishing effort than that used by Walters and Buckingham (1975).

However, it is not likely that we can ever capture a major portion of the $1 040 000 in benefits that are foregone in the Nass River sockeye fishery because of imperfect control over harvesting. As our model has shown, this is because of the spatial and temporal dynamics of the fish stock, the fishing fleet, the escapement monitoring program, and the decision-making process, as well as the variability in these components.

The observed differences between the historical data (i.e., average escapement, catch, and total recruits in the first row of Table 2) and simulation results (rest of Table 2) likely resulted from several factors. First, the simulation results represent a much larger sample size than the 11 years of historical data for which we have estimates of all catch categories. Second, we did not include the use of the commercial *C/f* in the model's decision-making routine. Although this information has only recently been used rigorously (D. Peacock, personal communication) to manage the area 3-12 fishery, very abundant runs were occasionally detected in the past using the commercial fishery *C/f* and managers reacted by extending openings earlier in the season than the model would predict. Finally, labour disputes occurred in at least two seasons of the historical data set, resulting in no fishing for portions of the season. Despite these differences between actual and modeled performance, the comparison between escapement monitoring techniques in this paper was internally consistent; in our comparisons, all other factors were held constant except for the methods of monitoring the escapement. Our purpose was not to mimic the historical situation, which clearly would have been impossible for the reasons noted above, but rather to use a reasonably realistic model to estimate the expected change in catch that would result from changing the method of in-season monitoring of escapement. The model was therefore a useful tool for estimating the expected benefits of improving escapement monitoring.

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References

Adkison, M.D., Peterman, R.M., Lapointe, M.F., Gillis, D.M., and Korman, J. 1996. Alternative models of climatic effects on sockeye salmon productivity in Bristol Bay, Alaska, and the Fraser River, British Columbia. Fish. Oceanogr. **5**: 137–152.

Bannerot, S.P., and Austin, C.B. 1983. Using frequency distributions of catch per unit effort to measure fish-stock abundance. Trans. Am. Fish. Soc. **112**: 608–617.

Bocking, R.C., and Peterman, R.M. 1988. Preseason forecasts of sockeye salmon (*Oncorhynchus nerka*): comparison of methods and economic considerations. Can. J. Fish. Aquat. Sci. **45**: 1346–1354.

Cox-Rogers, S., and Jantz, L. 1993. Recent trends in the catchability of sockeye salmon in the Skeena River gillnet test fishery, and impacts on escapement estimation. Can. MS Rep. Fish. Aquat. Sci. No. 2219.

Crecco, V.A., and Savoy, T.F. 1985. Density-dependent catchability

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and its potential causes and consequences on Connecticut River American shad. Can. J. Fish. Aquat. Sci. **42**: 1649–1657.

Donaldson, I.J., and Cramer, F.K. 1971. Fishwheels of the Columbia. Binfords and Mort, Portland, Oreg.

Eggers, D.M. 1992. The benefits and costs of the management program for natural sockeye salmon stocks in Bristol Bay, Alaska. Fish. Res. **14**: 159–177.

Eggers, D.M. 1993. Robust harvest policies for Pacific salmon fisheries. *In* Proceedings of the International Symposium on Management Strategies for Exploited Fish Populations. *Edited by* G. Kruse, D.M. Eggers, R.J. Marasco, C. Pautzke, and T.J. Quinn II. Alaska Sea Grant College Program Rep. No. 93-02, University of Alaska–Fairbanks, Fairbanks, Alaska. pp. 85–106.

Francis, R.C., and Hare, S.R. 1994. Decadal-scale regime shifts in the large marine ecosystems of the north-east Pacific: a case for historical science. Fish. Oceanogr. **3**: 279–291.

Fried, S.M., and Hilborn, R. 1988. In-season forecasting of Bristol Bay, Alaska, sockeye salmon (*Oncorhynchus nerka*) abundance using Bayesian probability theory. Can. J. Fish. Aquat. Sci. **45**: 850–855.

Henderson, M.A., Peacock, D., and Goruk, R. 1987. Evaluation of the reliability of several models used to forecast the size of adult sockeye salmon (*Oncorhynchus nerka*) runs. *In* Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. *Edited by* H.D. Smith, L. Margolis, and C.C. Wood. Can. Spec. Publ. Fish. Aquat. Sci. No. 96. pp. 266–272.

Hilborn, R.1985. Fleet dynamics and individual variation: why some people catch more fish than others. Can. J. Fish. Aquat. Sci. **42**: 2–13.

Holling, C.S. 1959. Some characteristics of simple types of predation and parasitism. Can. Entomol. **91**: 385–398.

Kendall, M.G., and Stuart, A. 1967. The advanced theory of statistics. Vol. 2. Inference and relationship. Charles Griffin, London, England.

Link, M.R. 1995. The value of an improvement in the precision and accuracy of information used to manage a sockeye salmon (*Oncorhynchus nerka*) fishery: the Nass River gillnet and fishwheel test fishery programs. Rep. No. 164. Master's thesis, School of Resource and Environmental Management, Simon Fraser University, Burnaby, B.C.

Link, M.R., and English, K.K. 1996. The 1993 fishwheel program on the Nass River and an evaluation of fishwheels as an in-season management and stock assessment tool for the Nass River. Can. Tech. Rep. Fish. Aquat. Sci. No. 2130.

Link, M.R., English, K.K., and Bocking, R.C. 1996. The 1992 fishwheel program on the Nass River and an evaluation of fishwheels as an in-season management and stock assessment tool for the Nass River. Can. MS Rep. Fish. Aquat. Sci. No. 2372.

Lord, G.E. 1976. Decision theory applied to the simulated data acquisition and management of a salmon fishery. Fish. Bull. U.S. **74**: 837–846.

Meehan, W.R. 1961. Use of a fishwheel in salmon research and management. Trans. Am. Fish. Soc. **90**: 490–494.

Minard, R.E., and Meacham, C.P. 1987. Sockeye salmon (*Oncorhynchus nerka*) management in Bristol Bay, Alaska. *In* Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. *Edited by* H.D. Smith, L. Margolis, and C.C. Wood. Can. Spec. Publ. Fish. Aquat. Sci. No. 96. pp. 336–342.

Noakes, D.J. 1989. A nonparametric approach to generating in-season forecasts of salmon returns. Can. J. Fish. Aquat. Sci. **46**: 2046–2055.

Paulik, G.J., and Greenough, J.W., Jr. 1966. Management analysis for a salmon resource system. *In* Systems analysis in ecology. *Edited by* K.E.F. Watt. Academic Press, New York. pp. 215–252.

Pearse, P.H. 1982. Turning the tide. A new policy for Canada's Pacific fisheries. The Commission on Pacific Fisheries. Final Report. Ministry of Supply and Services, Ottawa, Ont.

Peterman, R.M. 1981. Form of random variation in salmon smolt-to-adult relations and its influence on production estimates. Can. J. Fish. Aquat. Sci. **38**: 1113–1119.

Peterman, R.M., and Steer, G. 1981. Relations between sport-fishery catchability coefficient and salmon abundance. Trans. Am. Fish. Soc. **110**: 585–593.

Peterman, R.M., Steer, G., and Bradford, M.J. 1985. Bias in estimating density dependent catchability due to imprecise abundance estimates. Trans. Am. Fish. Soc. **114**: 436–440.

Ricker, W.E. 1973. Linear regressions in fishery research. J. Fish. Res. Board Can. **30**: 409–434.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. No. 191.

Shardlow, T., and Hilborn, R. 1985. Bias in estimating density dependent catchability due to imprecise abundance estimates. Trans. Am. Fish. Soc. **114**: 436–440.

Southgate, D.R., Spilsted, B., and Jantz, L. 1990. A review of the Nass River test fishery biological program for 1989. Can. Data Rep. Fish. Aquat. Sci. No. 805.

Sprout, P.E., and Kadowaki, R.K. 1987. Managing the Skeena River sockeye salmon (*Oncorhynchus nerka*) fishery — the process and problems. *In* Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. *Edited by* H.D. Smith, L. Margolis, and C.C. Wood. Can. Spec. Publ. Fish. Aquat. Sci. No. 96. pp. 385–395.

Steer, G.J. 1988. Value of information in Pacific salmon (*Oncorhynchus* spp.) fishery management: the Skeena River test fishery. Rep. No. 66. Master's thesis, School of Resource and Environmental Management, Simon Fraser University, Burnaby, B.C.

Walters, C.J., and Buckingham, S. 1975. A control system for intra-season salmon management. *In* Proceedings of a Workshop on Salmon Management, February 24–28, 1975. International Institute for Applied Systems Analysis, Laxenburg, Austria. CP-75-2. pp. 105–137.

Winters, G.H., and Wheeler, J.P. 1985. Interaction between stock area, stock abundance, and catchability coefficient. Can. J. Fish. Aquat. Sci. **42**: 989–998.

Wright, S. 1981. Contemporary Pacific salmon fisheries management. N. Am. J. Fish. Manage. **1**: 29–40.

Appendix.

Testing for the density-dependent catchability coefficient, q, for the gillnet test fishery

Errors in the measurement of the annual escapement may affect our assessment of whether the catchability coefficient, q, for the gillnet test fishery is density dependent because normal regression methods are biased when the independent variable is measured with error (Kendall and Stuart 1967). This problem is particularly acute when dealing with the usually imprecise estimates of salmon escapement (Peterman and Steer 1981; Peterman et al. 1985; Shardlow and Hilborn 1985). In the case of estimating the degree of nonlinearity of the relationship between C/f and N in the gillnet test fishery (eq. 4), errors in the annual escapement estimate may cause one to conclude that the relationship is nonlinear (i.e., q is density dependent, Peterman and Steer 1981) when in fact it is linear (i.e., q is constant, Shardlow and Hilborn 1985). Ricker (1973) recommended using functional regression to try to minimize this problem when the independent variate is measured with error.

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We used both ordinary least squares (OLS) and geometric mean functional (GMF, Ricker 1973) regression of $\log_e(C/f)$ on $\log_e(N)$ to test the hypothesis that $\beta_3 = 1$ (eq. 4). Regressions of the log-transformed variates by both OLS and GMF were significant (OLS: $\beta_3 = 0.43$, GMF: $\beta_3 = 0.54$; $n = 27$, OLS, GMF: $P(\beta_3 = 1) < 0.001$) and the null hypothesis of linearity in the C/f versus N relationship was rejected (i.e., we concluded that q was density dependent). The 1992–1993 data appear to have considerable leverage in this relationship (Fig. 4A); however, the null hypothesis that the C/f relationship was linear (i.e., q was density dependent) was still rejected even when these two years were excluded ($P(\beta = 1) < 0.01$).

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Detection of Atlantic herring (*Clupea harengus*) schools in shallow waters using high-frequency sidescan sonars

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Abstract: This work examines results from field trials in April and May 1996 exploring the feasibility for estimating spawning Atlantic herring (*Clupea harengus*) abundance using a 330-kHz sidescan sonar in a shallow coastal region near Escuminac, New Brunswick. Herring schools were observed using both towed and fixed-location, azimuthally scanning techniques at ranges up to 100 m in water depths of 3–6 m. The schools were typically linear in shape, with lengths of 100–280 m, thickness of 4–14 m, and peak acoustic target strength near –12 dB. Using acoustic ray-tracing analysis, surface- and bottom-reflected multipaths from an ensemble of targets are shown to increase the echo amplitude and reverberation time, producing large overestimates (4–27 times actual) in herring densities when using echo-integration. Using the acoustic simulations to compensate for this reflection focusing, average population densities near 11·m^{-3} were estimated, with the schools comprising 10 900 – 103 000 individuals. These total school sizes and densities were consistent with expectations for spawning herring.

Résumé : Les travaux portent sur les résultats des essais pratiques réalisés en avril et mai 1996 concernant la faisabilité d'évaluer l'abondance des harengs atlantiques (*Clupea harengus*) géniteurs au moyen d'un sonar latéral de 330 kHz, dans une région côtière peu profonde, près d'Escouminac au Nouveau-Brunswick. Des bancs de harengs ont été observés au moyen d'appareils de balayage en azimuth, remorqués et fixes, dont la portée pouvait atteindre 100 m par des profondeurs de 3 à 6 m. Les bancs étaient en général de forme linéaire, la longueur variant de 100 à 280 m, l'épaisseur de 4 à 14 m, et l'énergie acoustique maximale cible d'environ –12 dB. Grâce à la technique du tracé des rayons acoustiques, les trajets multiples réfléchis en surface et au fond d'un ensemble de cibles augmentent l'amplitude de l'écho et le temps de réverbération, ce qui produit des surestimations importantes (4 à 27 fois la valeur réelle) des densités de harengs lorsqu'on utilise l'échointégration. À l'aide des simulations acoustiques visant à équilibrer cette focalisation de réflexion, on a évalué les densités moyennes de la population à environ 11 poissons·m^{-3}, les bancs comptant 10 900 à 103 000 individus. Ces effectifs totaux et ces densités étaient conformes au nombre prévu de géniteurs.
[Traduit par la Rédaction]

Introduction

High frequency side-looking sonars offer a new approach for fish abundance measurement in shallow coastal regions. In shallow waters (depth <10 m), conventional vessel-based echo-sounding operations are generally limited due to the small sampling volume beneath the vessel and avoidance behaviour by the fish. In contrast, side-looking sonars have the advantage of a detection range many times that of the water depth, providing a much greater sampling volume and minimizing impacts on fish behaviour. Side-looking sonars have recently been utilized with some success for fish detection in rivers and lakes (e.g., Kubecka et al. 1994; Trevorrow 1997) and the open ocean (e.g., Hewitt et al. 1976; Rusby 1977; Misund 1993*a*, 1993*b*; Misund et al. 1995; Tarbox and Thorne 1996). However, complications arise with the side-looking geometry in shallow waters due to interference from boundary reverberation and the dependence of target strength (TS) on fish orientation relative to the beam (i.e., head, tail, or lateral incidence). In many previous side-looking applications, reverberation from surface and bottom boundaries has been specifically avoided by careful sonar beam steering and restricting the measurement range (typically <20 m). Problems with this approach are that the fish targets are commonly found very close to the boundaries, especially the bottom, and a greater sampling range is desirable.

This study investigated the applicability of high-frequency *sidescan* sonars to the problem of Atlantic herring (*Clupea harengus*) detection in a shallow coastal region. Such sidescan systems were originally devised for underwater surveys and navigation of remotely operated vehicles. In this study the sidescan beams were oriented such that they insonified the entire water depth in a narrow azimuthal slice, grazing and reflecting from both the surface and bottom boundaries. Both towed and fixed-location, azimuthally scanning techniques were investigated. In such shallow environments, acoustic scanning at greater range and grazing the boundaries necessarily invited backscattered interference from bottom sediments, surface roughness, breaking waves, and boat wakes. An additional complication was the acoustic focusing effects created by multiple reflections from the surface and bottom. Thus, the

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tasks herein are to quantify the fish echo strength relative to the background reverberation and to devise methods for compensating the observed echo strength for the reflection focusing effects.

This study was focused on detection of herring in shallow coastal waters. The Escuminac, New Brunswick, region was chosen because it has the largest and most consistent spring herring gillnet fishery in the southern Gulf of St. Lawrence. In late April and early May the herring come close inshore for spawning along a 10-km stretch of coastline in waters only 3–6 m deep (Messieh 1987). Aerial and scuba diver surveys have been attempted in this area, with some success in locating spawning beds and producing biomass estimates (Pottle et al. 1981; Messieh et al. 1985; Messieh and Pottle 1986). However, these surveys were not continued due to high costs and labour requirements. Ultimately, it is hoped that such sidescan sonar techniques could supplement traditional stock assessment approaches in shallow regions by providing in-season, fishery-independent abundance and exploitation indices collected directly from the fishing grounds. A particular advantage of fixed sonar installations is the ability to provide continuous monitoring, even through bad weather and fishery closures. This would help resolve criticisms from fishers that scientific stock assessments do not reflect abundance of local stocks.

Instrumentation and field operations

The field experiments were conducted between April 24 and May 22, 1996, near the fishing pier at Escuminac, N.B. A new 330-kHz azimuthally scanning sidescan built by Imagenex Technologies Inc. (Port Coquitlam, B.C.) was used. This sidescan system consisted of an underwater unit cabled to a remote surface control unit. The underwater unit consisted a rotating sidescan transducer and stepping motor, along with the signal generation and receiver electronics. The 330-kHz sidescan transducer had a fan-shaped beam, 1.8° in azimuth by 18° in the vertical plane (to –3dB), which could be steered azimuthally in 0.3° increments through ±180° from its home position. The pulse length was fixed at 100 μs, with a $20 \cdot \log_{10}(r) + 0.1 \cdot r$ (where r is range) time-variable gain applied to the received signal. The surface controller performed data acquisition and range averaging, generated a colour display on a VGA monitor, and stored raw data on a cartridge harddrive. The raw sonar echo was waveform detected and sampled at a base rate of 200 000 samples·s^{-1} with eight-bit resolution. Then, successive range samples were averaged to yield 7.5- to 10-cm resolution at ranges up to 200 m, with a typical pulse repetition period of 0.24–0.33 s. During the fixed-location, azimuthally scanning operations, this 330-kHz sidescan was set to scan a 360° disk to a range of 200 m with an angular step size of 0.9°. Thus, each 400-step, 360° sweep required 133 s to complete.

Two distinct types of tests were conducted: towed, wide-area surveys and long-duration, azimuthal scanning operations. Towed surveys were conducted from a 14-m coastal fishing vessel. The sidescan head was supported by a specially constructed towfish, which also included pitch, roll, heading, and depth sensors. The towfish locations and speeds were calculated using a GPS navigator. The sidescan transducer was mounted on the underside of the towfish pointing horizontally 90° to port, so that the towfish body blocked direct surface reflections. The towfish altitude above the seabed (to ±5 cm) was obtained from the earliest bottom echo. The towfish was deployed at depths of 1.5–2.5 m, suspended 2 m from the port side of the fishing vessel using a flexible wooden plank. The wooden plank damped wave-induced vessel motions (particularly roll), allowing the towfish to remain approximately level (tilts <3°) in the water. The typical towing speed was 2–5 knots, dependent on wind and wave conditions.

For the azimuthally scanning operations, the sidescan was deployed in front of an outer breakwater at the Escuminac fishing pier on April 29, 1996, in water depth of nominally 4.1 m (with ±0.2 m tidal range) on a specially constructed aluminum tripod. This tripod was designed to firmly support the rotating sidescan in rough, potentially breaking-wave conditions. The tripod base was an equilateral triangle of sides 1.75 m, with a pivoting central pedestal 0.95 m high. The rotating sidescan head was then located nominally 1.0 m above the seabed. After deployment the central pedestal was moved to a vertical position by a scuba diver using a bubble level. The deployment location was selected to avoid entanglement with fishery gill nets deployed in dense formations surrounding the Escuminac pier. The underwater surveying capabilities of the Imagenex system proved useful in determining the precise location and orientation of the tripod. One unfortunate aspect of this location was the concentration of fishing vessel traffic passing within 50 m of the tripod, particularly during early morning and middle evening. During sidescan operations, occasional water property profiles were collected with a SeaBird Electronics profiling CTD instrument. The typical water temperature and salinity in this coastal region were 0.0–4.5°C and 16.5–18.5 psu, respectively. Under these conditions the typical sound speed was near 1440 m·s^{-1}, roughly uniform with depth.

The sidescan system was calibrated utilizing the backscatter from tungsten-carbide target spheres (following Vagle et al. 1996). Separate calibration runs with three different sphere radii (19.05, 20.00, and 21.50 mm) were performed. The target spheres were suspended at several ranges from 5 to 15 m along the main axis of the transducer beam. Echo intensities were averaged over 200 transmissions. By comparing the calibration results from the three spheres at multiple ranges, the accuracy in TS measurements was estimated as ±0.5 dB. The transducer beam pattern was provided by the manufacturer and additionally verified with in situ tests. Then, including the calibration results, the variation of acoustic TS (decibels) at range r can be given by the well-known sonar equation (e.g., Clay and Medwin 1977)

$$(1) \quad \mathrm{TS} = K + 20 \cdot \log_{10}[A(r)] - \mathrm{TVG}(r) + 40 \cdot \log_{10}(r) + 2 \cdot \alpha \cdot r$$

where K is the calibration coefficient (which includes transmit power, transducer sensitivity, waveform detection, and A/D conversion factors), $A(r)$ is the echo amplitude, $\mathrm{TVG}(r)$ is the time-varying gain, and α is the acoustic absorption in seawater (=0.07 dB·m^{-1} at 330 kHz). Also, because of the limits of the ocean surface and seabed the effective insonified volume, U, for this sidescan beam increases only linearly with range (beyond the point where the beam intersects the boundaries, roughly 10 m range), i.e., as

$$(2) \quad U(r) = 0.5 \cdot c \cdot \tau \cdot d \cdot r \cdot \varphi$$

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where c is the sound speed (1440 m·s^{-1}), τ is the pulse length (100 μs), d is the water depth, and φ is the horizontal transducer beam angle (0.03142 rad).

The Escuminac region was an extremely active fishing area during late April and May, and the daily herring landings provided fish identity and size distribution information that supplemented the acoustic data. This inshore fishery used gill nets with mesh sizes from 5.7 to 6.4 cm (2.25–2.5 in.), 3 m high by 35 m long, with subsurface floats to support the top. These nets were typically deployed overnight, with the fish and nets retrieved in the early morning. Daily herring landings in the Escuminac area averaged 186 t through this period, ranging from a minimum of 2.75 t from one boat on April 25 to a maximum landing on May 14 of 1000 t. Total 1996 spring landings from the inshore gillnet fishery in the Escuminac management area were 5380 t, or about 30% of the total spring inshore landings in the southern Gulf of St. Lawrence. Samples taken from this fishery were used to compute seasonally averaged length-at-age population distributions for this region (Table 1). These distributions were adjusted for sample weight, landed weight associated with the sample, and landed weight in the fishery as described by Gavaris and Gavaris (1983). It was then assumed that the population distributions observed acoustically on a school by school basis were adequately represented by this seasonally averaged population. Finally, for abundance estimation purposes, this herring population can be represented by the weighted mean length of 29.0 cm. This neglects gillnet selectivity, specifically the undersampling of smaller fish classes, which has only a negligible effect on fish abundance based on this weighted mean length.

Foote (1987) reviewed a variety of in situ and laboratory measurements and presented an empirical relationship for Atlantic and North Sea herring for 38-kHz echo sounders of the form TS (decibels) = $20 \cdot \log_{10}(L) - 71.9$ where L is the fish length (centimetres). Using this relationship, the mean length of Escuminac herring corresponds to an acoustic TS at *dorsal* incidence, TS_{dorsal}, of –42.5 dB. Unfortunately, the literature on herring TS at higher frequencies is ambiguous. Strictly, the use of a $20 \cdot \log_{10}(L)$ relationship implies a geometric scattering regime, i.e., with no frequency dependence. Measurements by Rudstam et al. (1988) showed an increase in herring TS (–40.6 dB for L = 29 cm) at 70 kHz. However, empirical results from a large number of fish species (including clupeoids) compiled by Love (1977) indicate a modest decrease in TS at higher acoustic frequencies, with variation of $9 \cdot \log_{10}(\lambda)$ where λ is the acoustic wavelength. In the absence of direct and reliable herring TS versus length relationships at the 330-kHz sidescan frequency, we shall assume the 38-kHz result to be applicable. Another important correction to TS accounting for the horizontal sonar incidence direction must be applied. Again, empirical evidence from Love (1977) revealed that the ratio between dorsal and azimuthally averaged horizontal incidence TS was –4.5 dB. Since in any given herring school composed of many thousands of individuals the fish are likely to have a wide range of incidence angles relative to the sonar beam, the use of an averaged horizontal TS_{fish} = –47.0 dB is appropriate.

Another effect that has the potential to bias echo-integrated school size is acoustic extinction by the herring. Toreson (1991) established an approximate absorption coefficient of 0.04 dB·m^{-1} on the basis of reduced intensity of bottom echoes beneath herring schools of similar density and fish size as observed here. Alternately, a rough estimate of fish extinction can be derived assuming that the herring extinction cross section is a multiple of the total scattering cross section. For an underwater air bubble (a crude yet workable model for fish scattering) at 330 kHz, this ratio of extinction to total scattering is 8.82 (see Clay and Medwin 1977). Using the herring TS of –47.0 dB yields a total scattering cross section of 2.51×10^{-4} m^2 and hence an extinction cross section $\sigma_e = 2.21 \times 10^{-3}$ m^2. Then the extinction within a fish school (α_{fish}, decibels per metre) is given by $4.34 \cdot N \cdot \sigma_e$ where N is the herring density (assumed 10·m^{-3}). Thus, we arrive at a herring school absorption of 0.1 dB·m^{-1} for these Escuminac herring schools. This extinction loss can be easily incorporated into the echo-integration calculations.

Table 1. Population length-at-age distributions estimated from fishery landings at Escuminac, N.B., from April 25 to May 23, 1996.

Age (years)	Catch numbers	Mean length (cm)
3	52	25.3
4	494	28.0
5	17 417	28.3
6	2 251	29.2
7	3 972	29.9
8	3 938	31.1
9	784	30.8
10	51	32.7
11+	51	33.9
Weighted average		29.0

Observations with a towed sidescan

In this coastal environment the herring schools were widely dispersed and mobile, and thus were detected only occasionally. This was especially true in the earlier part of the season when, for example, during two days (April 25 and 26, 1996) of towed sidescan operations, only one clearly identifiable herring school was observed. This example will now be analyzed in detail.

A short raw data echogram versus range and time is shown in Fig. 1. The echogram shows a distinct herring school signature against a background of reverberation from the seabed (the sea surface at this time was calm). During this 2-min period the fishing vessel maintained a nominally constant course and speed of 2.4 m·s^{-1}. The sidescan was oriented 90° to port, transmitting once every 0.24 s. This school was distinguished from the background reverberation by its motion and higher TS. In particular, note the high acoustic contrast at the near edge of the herring school. The school was observed at ranges of 42–65 m and had a thickness of 4–15 m and length roughly 280 m (assuming the school was stationary). Attempts to circle around and view the school at closer range startled the herring school into motion. The school clearly exhibited boat avoidance behaviour as we chased it into deeper waters, highlighting the impracticality of vertical echo-sounding in these shallow waters. The vessel speed and transmission interval implied a 0.58-m along-track resolution, providing a moderate amount of overlap between successive acoustic transmissions, especially at greater range. The first bottom return shows the

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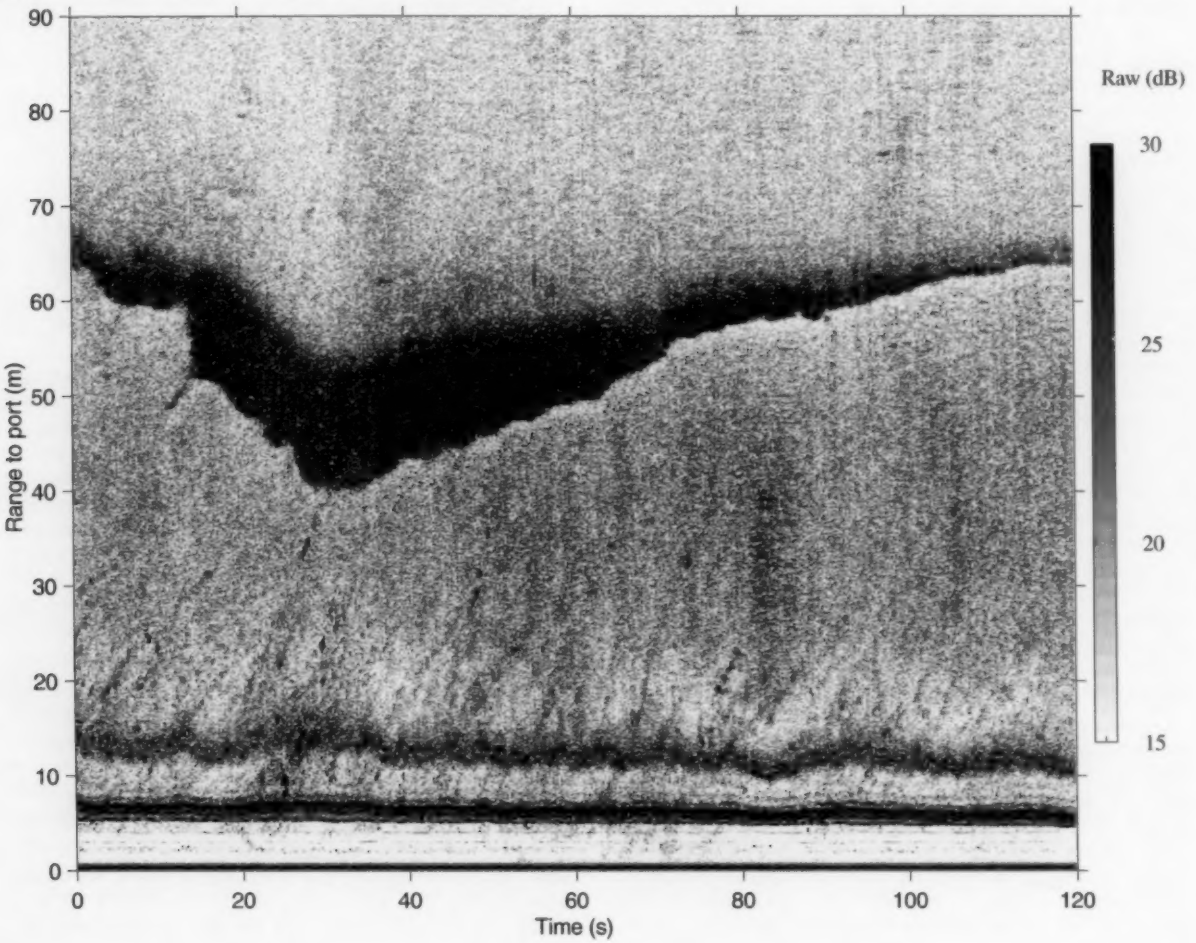
Fig. 1. Raw backscattered intensity versus range and time taken with the 330-kHz sidescan in the towed configuration. Data start at 14:46 on April 26, 1996. Towfish speed was 2.4 m·s^{-1} heading 229° true.



towfish altitude above the seabed to be 4.5 m. At this time the towfish depth was 1.7 m, so the total water depth was 6.2 m. Note that the clarity of detection of this school was aided by a relatively low level of background seabed scattering and calm surface conditions.

This last point is better seen through a quantitative comparison of background reverberation curves from towed sidescan operations over sandy and rocky bottom types (Fig. 2). The bottom types were determined from consultation with nautical charts and local fishers. TS profiles were calculated from raw data using eq. 1. The profile through the herring school revealed a 10-dB TS to reverberation ratio (TSRR) over this sandy seabed. However, this same herring school would have been scarcely visible over the rocky bottom at the same range. These background reverberation curves are important, as they define a range-dependent threshold for echo-integration analysis. Specifically, the integration region through the herring school can be defined where the measured TSRR is more than 3.0 dB. Then, for a given profile of TS versus range, the total number of herring, N, can be calculated using

$$(3) \quad N = \int_{\text{school}} 10^{0.1(\text{TS}-\text{TS}_{\text{fish}}+\text{TL}_{\text{fish}})} \cdot \mathrm{d}r$$

where dr is the range increment (in this case 7.6 cm), TL_{fish} is the acoustic extinction within the fish school ($=2\cdot\alpha_{\text{fish}}(r - r_0)$ where r_0 is the start range of the school), and the integral is evaluated only when the TS threshold is exceeded. In this example the integrated number of herring contained in the profile is 4280, with *apparent* herring densities in the range 180–820·m^{-3}. These are drastically higher than previously reported values for pelagic herring schools near 4·m^{-3} (Misund 1993*b*; Misund et al. 1995) and suggest that acoustic reflection focusing effects could be important. Since the sidescan beam dimension at 50 m range is 1.6 m, or roughly three times the along-track resolution, averaging over three successive transmissions should produce nominally independent samples. Integrating over all the independent profiles in the herring school shown in Fig. 1, the apparent total number of herring observed is 624 000. Since the total volume of the school (integrating $U(r)$ similarly to eq. 3, but assuming that the herring fill only 75% of the water depth) is 10 200 m^3, this produces an

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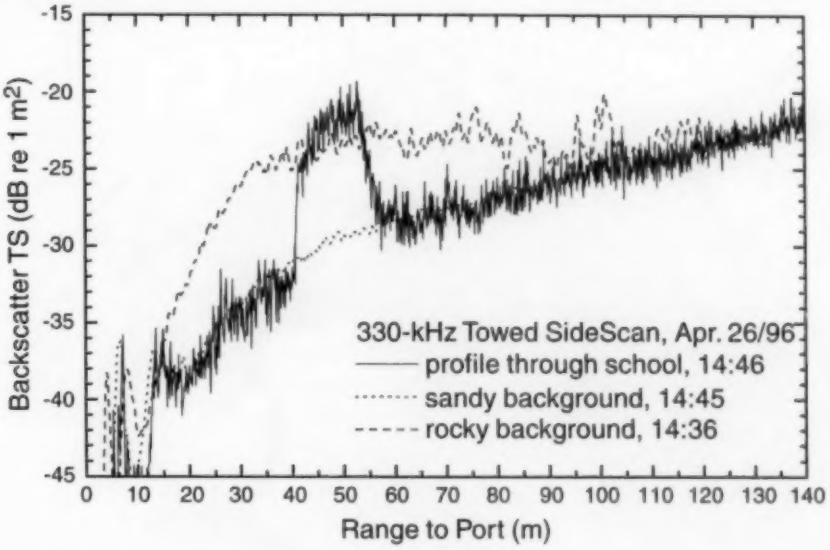
Fig. 2. Comparison of 330-kHz TS profile through the herring school shown in Fig. 1 with background reverberation levels from sandy and rocky seabeds. Profile through herring school averaged over 10 transmissions (2.4 s) at time = 30 s in Fig. 1. Background reverberation curves averaged over 200 transmissions (48 s).



apparent overall density of 61.2·m^{-3}, which is again considerably higher than expectations.

The seabed reverberation versus range curves should increase proportional to the insonified area, i.e., as

$$(4) \quad TS_{seabed} = SS(\phi) + 10\cdot\log_{10}(0.5\cdot c\cdot\tau\cdot\varphi\cdot r\cdot\cos\phi)$$

where $SS(\phi)$ is the seabed scattering strength (decibels) at grazing angle ϕ, which for sandy sediments at grazing angles <10° takes values near –38 dB (Wong and Chesterman 1968). Using this value of $SS(\phi)$ and pulse length and beam width values for this sidescan, eq. 4 can be reduced to $TS_{seabed} = -65.5 + 10\cdot\log_{10}(r)$. The actual least-squares fit to the sandy seabed reverberation curve ($30 < r < 140$ m) in Fig. 2 is $TS_{fit} = -56.5 + 15.6\cdot\log_{10}(r)$ (correlation coefficient = 0.991), which increases more rapidly with range than postulated by eq. 4. This can be attributed to the effects of acoustic multipath reflections (discussed below), which increase both the echo amplitude and effective pulse length. Conversely, the rocky seabed reverberation curve attained a roughly constant TS_{seabed} from 40 to 140 m range, implying a decrease in $SS(\phi)$ as the grazing angle decreases at greater range. This is plausibly due to acoustic shadowing by the rougher seabed interface.

Observations with an azimuthally scanning sidescan

The azimuthally scanning sidescan produced a time series of two-dimensional images up to 200 m range in front of the Escuminac pier. In this geometry, herring school activity could be recognized by searching for objects that moved relative to the stationary seabed. This region had water depths almost uniformly 4.1–4.3 m deep, 30% shallower than for the towed example previously discussed. Figure 3 shows an example (raw data) echogram of two herring schools detected with the rotating sidescan system on the morning of May 14. One herring school (denoted by the letter A in Fig. 3) moved from the breakwater location (linear object 35–40 m southeast of the origin), curving northeasterly and joining a second larger school (denoted by the letter B) at a range of 65 m. The smaller school had a maximum width of 4.5 m and an arc length of roughly 40 m. The larger school exhibited a roughly linear shape oriented west–northwest – east–southeast at a range of 60–70 m. The maximum width of the larger school was roughly 8 m with a length of approximately 80 m. The detection of these two schools was again aided by calm weather conditions and a relatively low-intensity seabed backscatter regime, due to a region of smooth sand in a swath roughly 60 m out from the breakwater. At greater range (especially to the west and northwest), there were more intense backscatter features (gravely or rocky seabed) that could obscure such herring schools.

Again, the background reverberation levels set limits on the detectability of herring schools with this system. Figure 4 shows the background reverberation curves calculated by averaging echoes within an 11° sector over multiple sidescan sweeps when there were no herring present. Here, we compare data from a period of wind and breaking waves (wind speed estimated at roughly 20 knots) on the previous day with a sector through the larger herring school shown in Fig. 3. Encouragingly, the herring school at 65–75 m range revealed a TSRR up to 17 dB under calm conditions and up to a 12 dB under windy conditions. The maximum observed TS in the school reached –13 dB at 64 m range, corresponding to an apparent herring density of 4450·m^{-3}. Computing the integrated number of herring in the two schools shown in Fig. 3 yields an apparent total of 250 000 fish and a total school volume of 930 m^3, for an apparent average density of 269·m^{-3}. This herring density estimate is clearly unreasonably high.

At close range (<60 m) the backscattered reverberation level under calm conditions was similar to that observed in the

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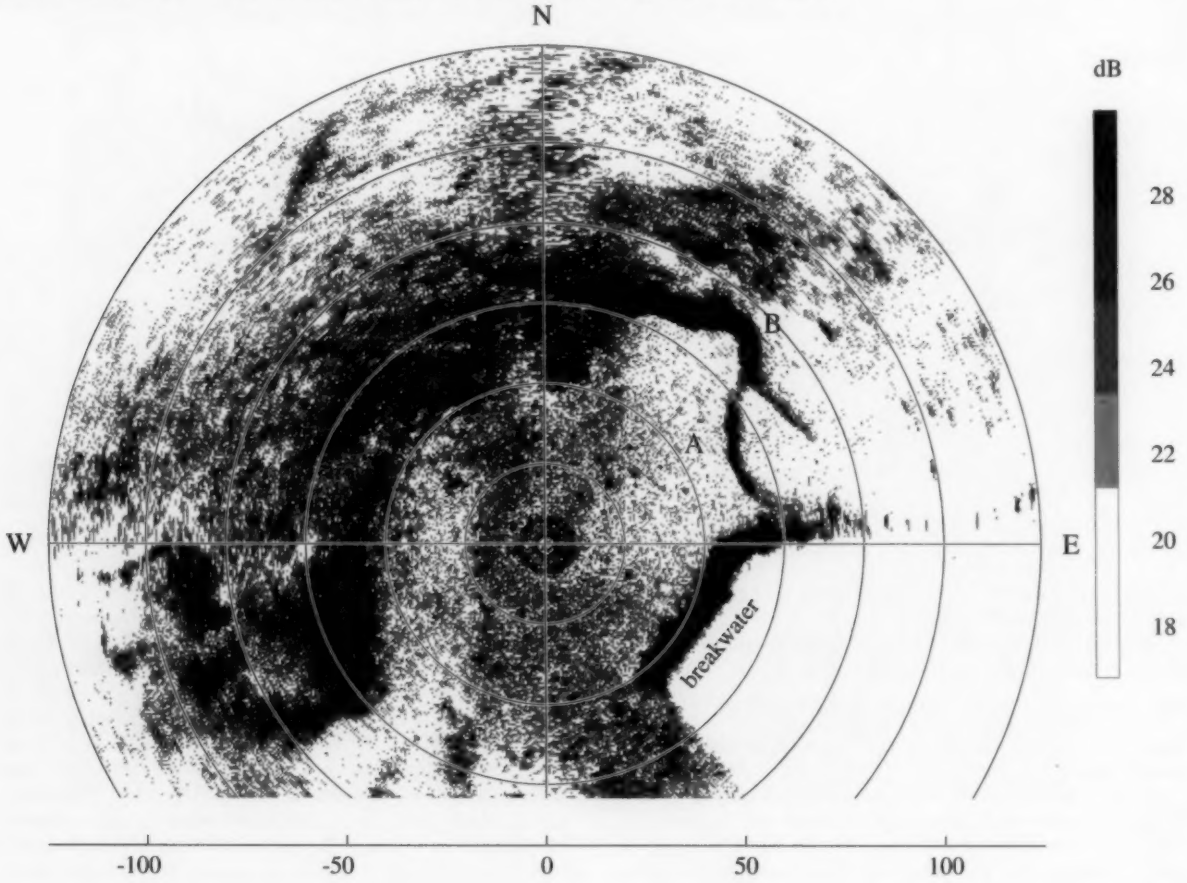
Fig. 3. Raw backscattered intensity versus range and azimuth from the 330-kHz sidescan taken at 06:53 on May 14, 1996. Image is composed of 400 separate transmissions with 0.9° angular spacing taken over 133 s. Bottom scale indicates distance (m). Image shows breakwater at 40 m southeast and two herring schools, denoted by A and B, in the northeast quadrant near 60 m range.



towed sidescan case. However, the fitted reverberation curve ($TS_{fit} = -76.0 + 26.3 \cdot \log_{10}(r)$, $40 < r < 180$ m) increased more strongly with range. Again, the fact that this seabed backscattering increased more rapidly than postulated by eq. 4 is suggestive that reflection focusing effects are present. The windy conditions induced an increase in backscattered reverberation of up to 5 dB (at close range) due to a tenuous layer of small air bubbles injected near the surface by breaking waves (see Trevorrow 1997).

Reverberation simulations using acoustic ray-tracing

The presence of reflecting surface and seabed boundaries in these shallow-water environments adds an additional acoustic propagation effect that must be included in any quantitative estimates of herring target densities. In essence the shallow-water environment acts as a form of *acoustic waveguide* that focuses more acoustic energy on the target and receiver while also increasing the *effective* pulse length relative to an unbounded medium. Earlier, it was found that herring school densities calculated without including these reflection effects were unreasonably high. In the case of isolated target scattering (e.g., salmon in a river), it is possible in most cases to separate the direct and reflected multipaths by using a very short transmit pulse (Trevorrow 1997). However, for the case of a herring school in shallow water with many thousands of targets closely spaced, the direct and reflected multipaths are not separable. Furthermore, the quantitative nature of the reflection focusing effects will be sensitive to the sidescan and target depths, bathymetry, and water sound speed versus depth profiles.

It is well known that acoustic reflections from the sea surface will have negligible loss and a 180° phase shift at all angles of incidence (Clay and Medwin 1977). What is generally not appreciated is that typical sandy or rocky seabeds will also give nearly perfect reflections at small grazing angles. For acoustic reflection at an interface between two media (denoted 1 and 2), Snell's Law takes the form $\cos\phi_1/c_1 = \cos\phi_2/c_2$ where ϕ is the grazing angle and c is the sound speed. For $c_2 > c_1$, there will be perfect reflection with no phase shift for grazing angles less than $\arccos(c_1/c_2)$. Using realistic values of sound speed in the water (1440 $m \cdot s^{-1}$) and for sandy sediments

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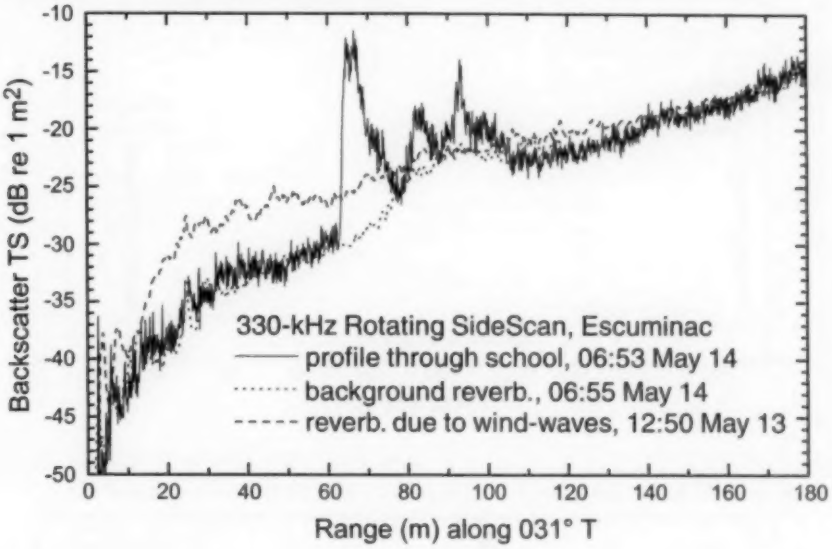
Fig. 4. Comparison of 330-kHz TS profile through the herring school shown in Fig. 3 with background reverberation levels under calm and windy conditions. Herring school profile averaged over an 11° angular sector oriented towards 031° true in Fig. 3. Background reverberation profiles averaged over 10 min within the same angular sector.



(1750 m·s^{-1}, Hamilton 1971), the reflection will be perfect at grazing angles <35°, which includes the large majority of multipaths in this shallow-water geometry.

At high frequencies, it is appropriate to model acoustic propagation using ray-tracing analysis (see Clay and Medwin 1997). Given the sound speed versus depth and bathymetry versus range data, ray-tracing calculations produce the ray trajectories, arrival times, launch and arrival angles, and amplitudes for all the possible *eigenrays* connecting the source and target. The various eigenrays must then have their amplitudes corrected for acoustic absorption loss (= α·ray path length) and sidescan transducer beam pattern losses on both transmit and receive. The sidescan transducer beam pattern closely approximated a rectangular source, with one-way angular variation of amplitude given by (Clay and Medwin 1977)

$$D(\theta) = \sin(0.5 \cdot k \cdot L \cdot \sin\theta)/(0.5 \cdot k \cdot L \cdot \sin\theta) \quad (5)$$

where θ is the angle from the main transducer axis, k is the acoustic wavenumber (=1440·m^{-1}), and L is the transducer vertical dimension (1.25 cm). With this specific beam pattern, rays launched or arriving at angles >±12° are greatly attenuated and thus ignored. Synthetic waveforms can now be generated by coherently adding the amplitude-corrected, time-shifted pulse replicas for each of the possible eigenrays. If there are n eigenrays connecting the source and target, then there are $n \times n$ possible two-way paths. To make the simulation of a herring school more realistic the synthetic waveforms for multiple targets in a cluster at slightly different locations were coherently added together. Then, to simulate the sidescan data acquisition process, the root mean square of the synthetic waveform was calculated at a sampling interval of 5 μs and then averaged over the pulse length (100 μs). Finally, echo-integration to extract the number of targets was performed in a manner similar to that used on the real acoustic data. The overall calculation was verified by simulating the direct-path waveform from a single target, which when integrated returned the correct answer of 1.0.

Figure 5 shows the geometry for a 16-target simulation of the towed sidescan example discussed in Figs. 1 and 2. The target range of 42 m corresponds to the near edge of the herring school shown in Fig. 2. The targets were spaced vertically at 0.2-m intervals from 3.0 to 6.0 m depth. For each of the 16 targets, there are three main eigenrays. A uniform sound speed of 1440 m·s^{-1} was used. Figure 6 compares the resultant synthetic waveforms for the full reverberation (including all three rays) and for the direct path only. Clearly, the effect of the reflected eigenrays is to increase the echo amplitude and extend the effective echo length. In this case the echo length is extended by about a factor of 3 over the direct-path echo. The resultant number of targets from root mean square averaging and echo-integration of these waveforms was 73.1 for the full reverberation and 16.6 for the direct path only. Thus, we can define a reflection enhancement factor, REF, which in this case takes a value 4.57. Repeating this simulation at 55 m range (the far edge of the herring school shown in Fig. 2) finds four main eigenrays and an integrated target size of 121.3, resulting in a REF of 7.58. Recalling the measured apparent school size of 624 000 herring and using an average REF of 6.06, the estimated *true* school size is now 103 000 herring with an average density of 10.1·m^{-3}.

This synthetic waveform calculation was repeated for the azimuthal scanning example discussed in Figs. 3 and 4. In this example the water was shallower and the herring school was located at a greater range. Figure 7 shows the sidescan and target geometry and the six main eigenrays for a school at 62 m range. A seventh eigenray appeared for targets located at or above 2.2 m depth. Figure 8 shows the comparison of the full reverberation and direct-path simulations for this geometry. In this example the integrated target size was 301, for a REF of 18.8. Repeating this calculation at 75 m range (the far edge of

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Fig. 5. Diagram of sidescan and multiple target geometry, showing three main eigenrays for one target, for the towed sidescan example shown in Figs. 1 and 2.

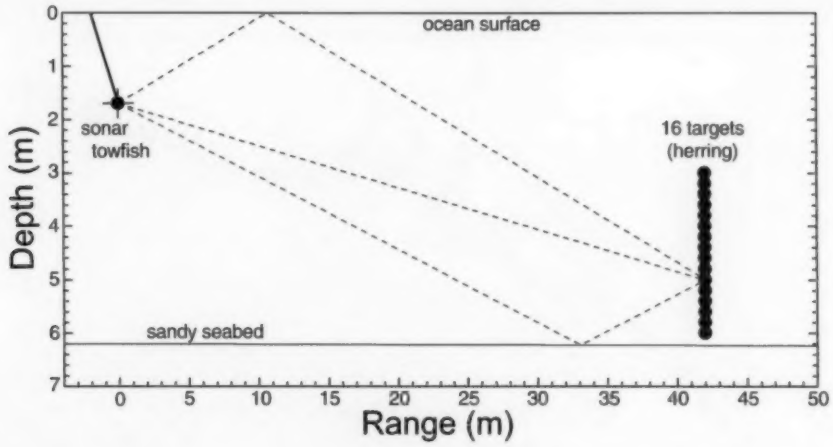
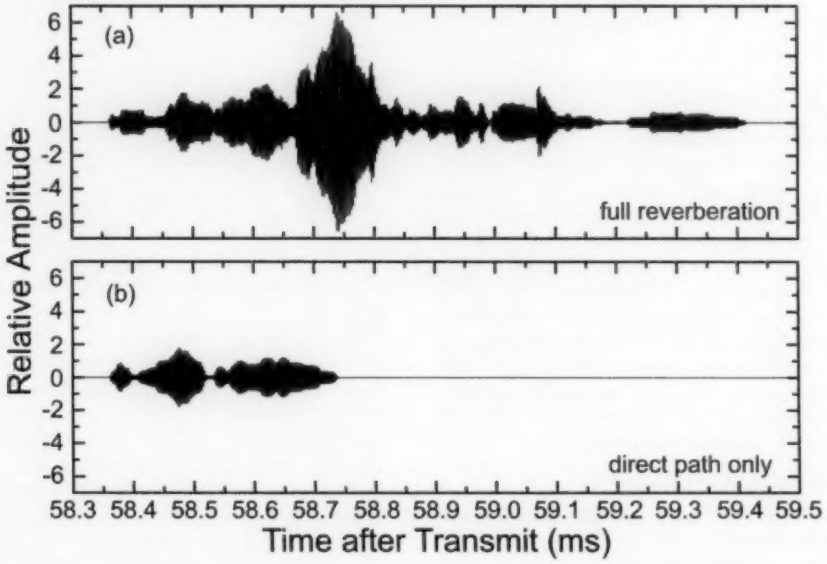


Fig. 6. Comparison of synthetic waveforms based on geometry shown in Fig. 5 for (*a*) full multipath reverberation (three eigenrays per target) and (*b*) direct path only simulations of backscattering from 16 targets at depths from 3.0 to 6.0 m at a range of 42 m.



the school) including seven or eight eigenrays yielded an integrated target size of 432 (REF = 27.0). Recalling the measured total school size of 250 000 and using an average REF of 22.9, the estimated true school size is now 10 900 herring, for an average density of 11.7·m^3. Note that the average density estimates for these two schools are now quite close, even though they differ in total school size by a factor of 10.

Discussion

Review of the many hours of 330-kHz sidescan data from the Escuminac site uncovered many clear examples of herring schools detected in waters only 3–6 m deep, of which two examples are analyzed in detail herein. These herring schools were recognized by a combination of their greater TS and dynamic behaviour against a stationary, relatively featureless reverberation from sandy seabeds. Quantitative analysis demonstrated a 10- to 17-dB detection signal to reverberation ratio under calm conditions with sandy bottom sediments. The towed sidescan operations had the advantage of wide areal coverage whereas the azimuthally scanning operations provided long-duration surveillance of a fixed area 400 m in diameter. Both methods provide additional behavioural information on herring school size, shape, and speed of movement.

With the herring sizes known from fishery samples, calculations from two herring schools yielded densities of 10.1 and 11.7·m^{-3} with total school sizes of 10 900 – 103 000 fish.

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Fig. 7. Diagram of sidescan and multiple target geometry, showing the six main eigenrays for one target, for the azimuthal sidescan example shown in Figs. 3 and 4.

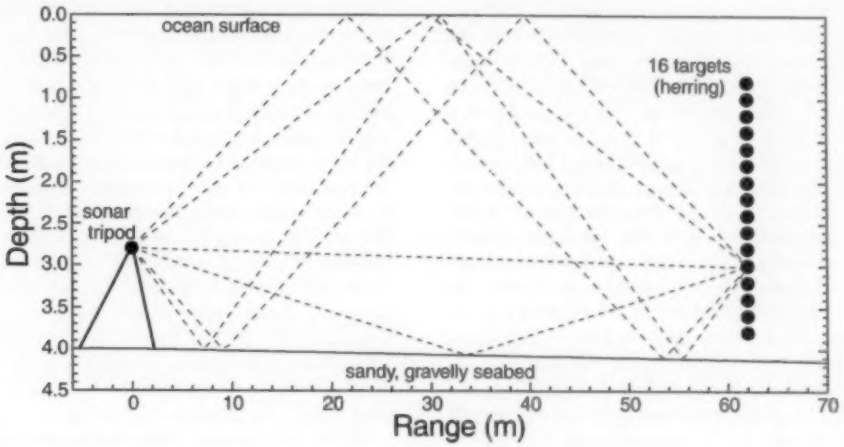
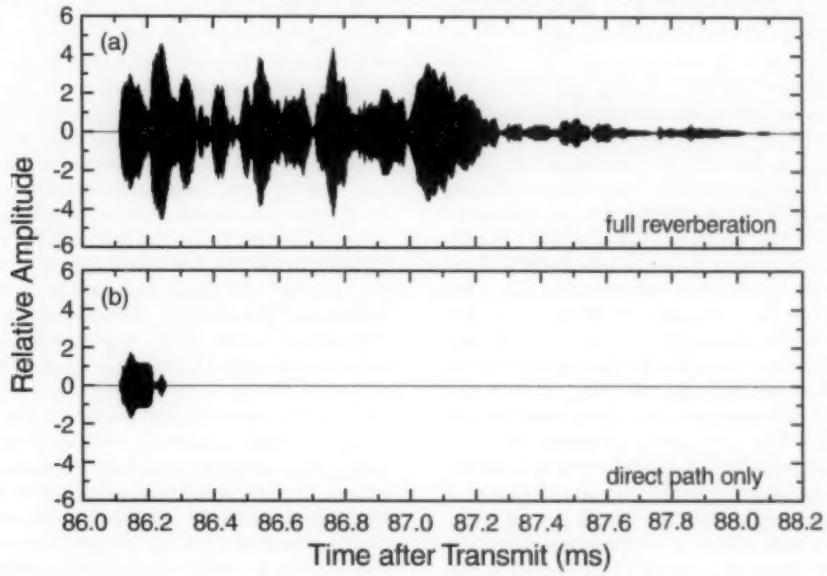


Fig. 8. Comparison of synthetic waveforms based on geometry shown in Fig. 7 for (*a*) full multipath reverberation (six or seven eigenrays per target) and (*b*) direct-path simulations of backscattering from 16 targets at depths from 0.8 to 3.8 m at a range of 62 m.



These densities were roughly three times higher than the *average* school density of 4.25·m^{-3} reported by Misund (1993*b*) and Misund et al. (1995) for 29-cm herring in the North Sea and along the Norwegian coast. However, Misund's work reported herring school densities in the range 0.3–22·m^{-3} with mean school sizes from 21 000 to 153 000 fish. Similar pelagic adult herring densities have been observed from vessel-based acoustic surveys conducted yearly in October in the southern Gulf of St. Lawrence, following the fall spawning season and just prior to overwinter migrations (reported in Claytor et al. 1997). The typical densities for postspawned adults observed during such surveys from 1990 to 1996 were 1–4·m^{-3}; however, densities of prespawning juveniles of up to 10·m^{-3} were observed. The typical school sizes observed in those autumnal pelagic surveys were 2000 – 136 000 fish. Thus the two observations presented herein suggest that spawning herring schools in *shallow waters* have similar overall size but are more tightly packed than those found in pelagic regions. This seems entirely reasonable, but a more thorough examination through simultaneous sidescan imaging and direct net capture of the herring schools is required to establish this difference in density.

It was demonstrated using acoustic ray-tracing analysis that the presence of surface and seabed reflected multipaths produces an upward bias in the received echo strength from a collection of targets (such as a herring school). Experimentally, an upward bias due to such reflection focusing effects was found in two ways. Firstly, the measured apparent herring

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school densities (averaging 61–269·m^{-3}) were unrealistically high. Secondly, the seabed backscatter versus range curves increased more rapidly with range (proportional to $r^{1.56}$ and $r^{2.63}$) than predicted by simple models. Additionally, both the measured and simulated reflection focusing effects were stronger in the shallower water case. For the towed sidescan example, simulations of this reflection focusing produced a REF of 4.5–7.5 at a ranges of 42–55 m in 6.2 m water depth. This REF was found to increase at greater range and in shallower water through the inclusion of more eigenrays within the main lobe of the transducer beam. For example, in 4.1 m water depth near 70 m range the REF was 23. The ray-tracing waveform simulations outlined herein provide a method for estimating the REF for each specific target range, water depth, and sound speed profile. Knowledge of the REF then allows accurate school size assessment at moderately large range, conceivably of order 200 m, in these shallow-water environments.

A critical requirement for accurate school sizing is knowledge of the acoustic TS of the individual fish. For the case of dorsal incidence at 38 kHz the TS versus length relationship for herring is well established. However, there is a need to measure TS for herring at other frequencies and incidence angles. At horizontal incidence the TS of an individual herring (or herringlike fish) can vary by roughly 12 dB depending on orientation (i.e., head or tail versus lateral incidence). An average horizontal TS of –4.5 dB relative to the TS_{dorsal} (from Love 1977) seems appropriate for schooling fish with an unknown (and plausibly uniform) distribution of incidence angles. However, this assumption has the potential for biasing the population density estimates if the herring are all swimming at some *specific* orientation relative to the sonar beam. The two extrema are at lateral and head/tail incidence, corresponding to TS ratios of +1.5 and –11.0 dB relative to the dorsal value, respectively (Love 1977). These extremes of orientation would change, for example, the estimated size of the herring school shown in Fig. 1 to either 25 900 at lateral incidence or 460 000 at head/tail incidence. Clearly, it is important to be on guard for situations where the herring might be swimming in a uniform direction and adjust the TS_{fish} accordingly. For example, through examination of successive azimuthal images such as shown in Fig. 3, the mean swimming direction (and thus, mean fish orientation) of the school could be extracted.

Herring school detection is limited by the relative levels of herring school TS and (under calm conditions) seabed reverberation, with a minimum TSRR of 6.0 dB required for adequate detection. Both the herring school TS and reverberation levels should increase with range because of a combination of increased insonified area or volume (both as $10\cdot\log_{10}(r)$) and reflection focusing effects. As previously shown, the background reverberation levels increased as $15.6\cdot\log_{10}(r)$ and $26.3\cdot\log_{10}(r)$. However, the effective herring school TS increased with range at an equal or even greater rate due to the additional REF, which increases roughly linearly with range. Thus, the effective TSRR for a herring school actually *increases* with range. The limit to detection is then set by the electronic noise levels and time-varying gain limitations of the sonar system, which for this present 330-kHz sidescan was about 200 m.

A slightly different approach to herring stock assessment that does not rely on quantitative backscatter measurements and the associated compensation for reflection multipaths exploits an empirical relationship between school horizontal area and biomass (see Hewitt et al. 1976; Misund 1993*a*). Misund found a relationship between biomass (kilograms) and horizontal area (square metres) of the form $\log_{10}(\text{biomass}) = 1.33\cdot\log_{10}(\text{area}) + 0.43$ for pelagic herring and mackerel. However, in the pelagic case the fish schools could have a much greater vertical extent, so the area versus biomass relationship would need to be modified for this shallow coastal region. For the simple example of the two herring schools examined above (recognizing that only two measurements does not constitute a proper regression), the total school areas were 2200 and 300 m^2. The average mass of an individual herring of 29.0 cm length was 0.19 kg, producing biomass estimates of 19.6 and 2.07 t for these two schools. These two measurements then *suggest* a relationship of the form $\log_{10}(\text{biomass}) = 1.33\cdot\log_{10}(\text{area}) + 0.52$. Of course, this hypothesized relationship would need to be verified for these specific shallow-water conditions through a combined acoustic and net sampling field program.

Major interference from both boat wakes and breaking wave induced bubble clouds was often present. Intense backscattering regions were observed due to the injection of clouds of small, acoustically active air bubbles within vessel wakes. These wakes dissipated as the air bubbles either rose to the surface or dissolved into solution, a process that typically required 6–10 min (see Trevorrow et al. 1994). Also, newly created wakes *shadowed* acoustic backscatter from behind them, due to the strong acoustic absorption within the bubble clouds. In future experiments, it is advisable to select sidescan deployment sites far away from areas with boat traffic. However, bubble layers induced by winds and breaking waves are more pervasive, and no coastal location could be completely immune to this source of interference. Previous studies of breaking wave induced bubble plumes have found that they typically begin to appear under winds exceeding 5 m·s^{-1}, with bubble penetration depths increasing linearly with wind speed (Thorpe and Stubbs 1979). Bubble plumes in the open ocean have been observed to penetrate more than 10 m under winds >12 m·s^{-1} (Thorpe 1986). In the example shown here, an increase in background reverberation levels of up to 4 dB was observed under relatively modest winds. Under stronger winds, it is conceivable that bubble plumes could extend to the seabed, creating reverberation levels that seriously mask herring school detection. Tarbox and Thorne (1996) observed similar degraded detection performance with a near-surface, side-looking dual-beam system under windy conditions.

Acknowledgments

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References

Clay, C., and Medwin, H. 1977. Acoustical oceanography: principles and applications. Wiley-Interscience, New York.

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Claytor, R., LeBlanc, C., Sinclair, A., Poirier, G., and Paulin, L. 1997. Assessment of the NAFO Division 4T Atlantic herring stock, 1996. DFO Canadian Stock Assessment Secretariat Research Document 97/30.

Foote, K. 1987. Fish target strengths for use in echo integrator surveys. J. Acoust. Soc. Am. **82**: 981–987.

Gavaris, S., and Gavaris, C. 1983. Estimation of catch-at-age and its variance for groundfish stocks in the Newfoundland region. *In* Sampling commercial catches of marine fish and invertebrates. *Edited by* W. Doubleday and D. Rivard. Can. Spec. Publ. Fish. Aquat. Sci. No. 66. pp. 178–182.

Hamilton, E. 1971. Elastic properties of marine sediments. J. Geophys. Res. **76**: 579–604.

Hewitt, R., Smith, P., and Brown, J. 1976. Development and use of sonar mapping for pelagic stock assessment in the California Current area. Fish. Bull. U.S. **74**: 281–300.

Kubecka, J., Duncan, A., Duncan, W., Sinclair, D., and Butterworth, A. 1994. Brown trout populations of three Scottish lochs estimated by horizontal sonar and multimesh gill nets. Fish. Res. (Amst.), **20**: 29–48.

Love, R. 1977. Target strength of an individual fish at any aspect. J. Acoust. Soc. Am. **62**: 1397–1403.

Messieh, S. 1987. Some characteristics of Atlantic herring (*Clupea harengus*) spawning in the southern Gulf of St. Lawrence. North Atl. Fish. Org. Sci. Counc. Stud. **11**: 53–61.

Messieh, S., and Pottle, R. 1986. Distribution of gillnets and spring spawning grounds of Atlantic herring in the southern Gulf of St. Lawrence as inferred from aerial surveys. Fish. Res. Board Can. Tech. Rep. No. 1504.

Messieh, S., Pottle, R., MacPherson, P., and Hurlbut, T. 1985. Spawning and exploitation of Atlantic herring (*Clupea harengus*) at Escuminac in southwestern Gulf of St. Lawrence, spring 1983. J. Northwest Atl. Fish. Sci. **6**: 125–133.

Misund, O. 1993*a*. Abundance estimation of fish schools based on a relationship between school area and school biomass. Aquat. Living Resour. **6**: 235–241.

Misund, O. 1993*b*. Dynamics of moving masses: variability in packing density, shape, and size among herring, sprat, and saithe schools. ICES J. Mar. Sci. **50**: 145–160.

Misund, O., Aglen, A., and Fronaes, E. 1995. Mapping the shape, size, and density of fish schools by echo integration and a high-resolution sonar. ICES J. Mar. Sci. **52**: 11–20.

Pottle, R., MacPherson, P., Messieh, S., and Moore, D. 1981. A scuba survey of a herring (*Clupea harengus*) spawning bed in Miramichi Bay, N.B. Can. Tech. Rep. Fish. Aquat. Sci. No. 984.

Rudstam, L., Lindem, T., and Hansson, S. 1988. Density and in situ target strength of herring and sprat: a comparison between two methods of analysing single-beam sonar data. Fish. Res. (Amst.), **6**: 305–315.

Rusby, J. 1977. Long range survey of herring fishery by sidescan sonar. Rapp P.-v. Réun. Cons. Int. Explor. Mer, **170**: 7–14.

Tarbox, K., and Thorne, R. 1996. Assessment of adult salmon in near-surface waters of Cook Inlet, Alaska. ICES J. Mar. Sci. **53**: 397–401.

Thorpe, S. 1986. Measurements with an automatically recording inverted echo sounder: ARIES and the bubble clouds. J. Phys. Oceanogr. **16**: 1462–1478.

Thorpe, S., and Stubbs, A. 1979. Bubbles in a freshwater lake. Nature (Lond.), **279**: 403–405.

Toreson, R. 1991. Absorption of acoustic energy in dense herring schools studied by attenuation in the bottom echo signal. Fish. Res. (Amst.), **10**: 317–327.

Trevorrow, M.V. 1997. Detection of migrating salmon in the Fraser River using 100-kHz sidescan sonars. Can. J. Fish. Aquat. Sci. **54**: 1619–1629.

Trevorrow, M., Vagle, S., and Farmer, D. 1994. Acoustic measurements of microbubbles within ship wakes. J. Acoust. Soc. Am. **95**: 1922–1930.

Vagle, S., Foote, K., Trevorrow, M., and Farmer, D. 1996. Absolute calibrations of monostatic echosounder systems for bubble counting. IEEE J. Oceanic Eng. **21**: 298–305.

Wong, H.-K., and Chesterman, W. 1968. Bottom backscattering near grazing incidence in shallow water. J. Acoust. Soc. Am. **44**: 1713–1718.

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Gear-independent patterns of variation in catch of juvenile Atlantic cod (*Gadus morhua*) in coastal habitats

David A. Methven and David C. Schneider

Abstract: Habitat and size of juvenile Atlantic cod (*Gadus morhua*) change substantially during the first 3 years after settlement, and hence, cohort size cannot be followed using a single gear. We investigated whether catch could be calibrated across gear types by deploying pairs of gears repeatedly in the same habitat. As expected, size selectivity differed substantially among gears. Trawls and seines generally collected individuals <200 mm. Gillnets and jiggers collected individuals >150 mm. Size modes, corresponding to age-classes, were common to catches of most gears. Highest catches were taken by trawls and seines. Gillnet catches were orders of magnitude lower. Standardized catches could not be calibrated across pairs of gears deployed in the same habitat at approximately the same time. However, it was possible to identify spatial depth gradients and diel changes in catch that were independent of gear. Consistent spatial and temporal patterns across gears were interpreted as characteristic of fish populations, not just of gears. Density in coastal habitats was higher at night and was higher at 4–7 m than at greater depths. These results, in conjunction with other studies, establish that coastal depths of 4–7 m represent the centre, and not the edge, of the distribution of age 0 cod in Newfoundland during autumn. Hence nursery areas during the early 1990s, a time of historically low spawning stock biomass, must be identified as the coastal zone, not offshore.

Résumé : L'habitat et la taille des morues juvéniles (*Gadus morhua*) changent énormément au cours des 3 années qui suivent leur installation sur le fond; il est donc impossible de suivre l'effectif de la cohorte à l'aide d'un seul type d'engin. Nous avons tenté de savoir s'il était possible de calibrer les captures selon les types d'engins en mouillant des paires d'engins de façon répétitive dans le même habitat. Comme prévu, la sélectivité selon la taille différait considérablement d'un engin à l'autre. En général, les chaluts et les sennes prélevaient des spécimens mesurant moins de 200 mm, les filets maillants et les turluttes, des spécimens mesurant plus de 150 mm. Les modes de tailles, correspondant aux classes d'âge, étaient identiques pour les captures de presque tous les engins. Les captures les plus nombreuses ont été effectuées au chalut et à la senne. Les captures aux filets maillants étaient plus faibles de plusieurs ordres de grandeur. Les captures normalisées n'ont pu être calibrées par paires d'engins mouillés dans le même habitat à peu près au même moment. Toutefois, nous avons pu déterminer des gradients de profondeur spatialement définis et des changements nycthéméraux des captures indépendants de l'engin utilisé. Des profils spatiaux et temporels uniformes entre les engins ont été interprétés comme caractéristiques des populations de poisson, et pas seulement des engins. La densité dans les habitats côtiers était plus élevée la nuit, et plus élevée à des profondeurs comprises entre 4 à 7 m qu'à des profondeurs plus grandes. Ces résultats, combinés à d'autres études, montrent que les profondeurs côtières de 4 à 7 m correspondent au centre, et non pas à la lisière, de la distribution de la morue d'âge 0 à Terre-Neuve, à l'automne. Donc, au début des années 1990, période où la biomasse du stock reproducteur atteignait le plus bas niveau jamais enregistré, les aires d'alevinage correspondaient à la zone côtière et non à la zone du large.
[Traduit par la Rédaction]

Introduction

Recruitment variability and its prediction are important and longstanding problems in fisheries studies. Research has focused on early life stages because it is often theorized that year-class strength is established during a relatively brief critical period early in the life of fishes. Hjort (1914, 1926) hypothesized that year-class variability is related to a critical period in larval life when mortality is increased due to depletion of yolk and onset of starvation. Support for the critical period concept and for estimating recruitment from egg and larval surveys has not always been strong (May 1974; Cushing 1981; Peterman et al. 1988). An alternative view is that recruitment variability and cohort size are modified throughout the pelagic stage (Sette 1943) and continue to be modified during the first few years of life (Sissenwine 1984). This view places greater emphasis on tracking cohort strength throughout the juvenile stage.

Early juvenile stages of many marine fishes inhabit both pelagic and demersal environments where they are often segregated from adults (Harden Jones 1968). Consequently, a variety of sampling gears, some specifically designed, are required to measure juvenile abundance. In pelagic habitats, sampling early life stages of Atlantic cod (*Gadus morhua*) requires relatively few gears, some of which have been quantitatively compared (Schnack 1973; Solemdal and Ellertsen 1984; Suthers and Frank 1989; Potter et al. 1990). Such

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Table 1. Description of sampling sites and gear deployment in 1991 for comparisons of catches among gears.

Site	Location	Exposure[a]	Gear	Depth (m)	Substrate[b]
1. Bellevue	47°38′N, 53°43′W	Sheltered	1, 2, 3, 4, 5	1.5–4.0	Pebble, cobble, sand in deeper water
3. Beach	47°38′N, 53°46′W	Intermediate	1, 2, 4	7–12	Pebble, broken shells
4. Trap	47°39′N, 53°43′W	Exposed	1, 2, 4	5–30	Boulder, bedrock, sand in deeper water
5. Master's Head	47°43′N, 53°50′W	Intermediate	1, 6	6–10	Coarse sand to cobble
6. Bald Pt. Beach	47°50′N, 53°52′W	Intermediate	1, 6	6–25	Pebble, cobble, boulders in deeper water
7. Little Mosquito Cv.	47°50′N, 53°53′W	Sheltered	1, 6	3–8	Pebbles, mud
8. Deep	47°39′N, 53°46′W	Exposed	1, 2	18–35	Sand

Note: Gears: 1, gillnets; 2, trawl; 3, 9-m seine; 4, SCUBA; 5, 30.5-m seine; 6, 14-m seine. Site Nos. are those used throughout the text.
[a]Follows criteria in Steele (1983).
[b]Follows Wentworth scale (Lincoln et al. 1982).

Table 2. Gear characteristics for comparisons of catches among gears in 1991.

				Standardized catches		
Gear	A	t	n	LG0	LG1	LG2
30.5-m seine	73.2	0.08	1	0.78	3.90	0.32
9.0-m seine	8.2	0.05	2	4.15	4.15	0.17
14-m seine	21.0	0.06	3	6.34	3.43	0.10
Gillnets	54.9	≈15.00	3	0.00001	0.00082	0.001
SCUBA	9.0	≈0.36	1	3.31	2.82	0.06
4.9-m trawl	5.5	≈0.17	2	4.93	4.40	0.14

Note: A is the effective fishing area of a gear (m^2), t is the total time (h) gears were deployed (t was constant for beach seines and variable for other gears), and n is the number of nets (i.e., gillnets) deployed or, alternatively, the number of tows (i.e., trawls or beach seines) conducted for each gear comparison. Mean standardized catches ($fish \cdot m^{-2} \cdot h^{-1}$) are given for length groups of juvenile cod (LG0, LG1, LG2) as defined in the text.

comparisons have not been made for demersal stages, especially in coastal habitats where juvenile cod are often concentrated. Several difficulties arise when comparing catches among demersal samplers. These include differences between active and passive samplers (Hayes 1989; Hubert 1989), restrictions due to habitat type (Godø et al. 1989), and difficulties relating sampling effort to a standard unit (Ricker 1975, p. 19).

The initial objective of our study was to determine if catches of juvenile cod from contrasting coastal habitats could be calibrated among demersal gears (i.e., catch of one gear estimated from catch of a second gear). We used pairwise comparisons of standardized catches between simultaneously deployed gears in the same habitat to determine if calibration was possible. If catches can be calibrated across gears, it becomes possible to estimate losses from cohorts by sampling with different gear as individuals grow, become more mobile, and change habitat. A second objective was to test whether size modes were common across all gears. Early findings led to additional objectives where we tested whether spatial gradients of depth and temporal changes in catches were comparable across gears on a relative scale. If gradients are comparable, then pattern can be interpreted as characteristic of fish populations, not just of gear.

Methods

Most sampling was conducted at several shallow (usually <30 m) coastal sites using a 6-m open boat powered by a 45-hp outboard motor. Instrumentation included a speedometer (v, kilometres per hour through the water), depth sounder (z, metres), and clock (seconds). Cod caught by all sampling gears were counted and measured for standard length (SL, millimetres). All sampling gears are described in the Appendix and include several seines with different methods of deployment (9-, 14-, 25-, and 30.5-m seines), bottom trawl, gillnets, jigger, and visual observations by SCUBA divers. Depth was determined as the average of the depth at the start and finish locations for the bottom trawl and each gillnet and SCUBA dive. Depth was recorded as the maximum depth sampled for all of the seines, regardless of method of deployment.

Comparison of catches among gears

Sampling gears were deployed at several coastal sites in southern Trinity Bay, Newfoundland, from July to December 1991 (Table 1) to compare catch rates among gears. Catches were compared only for gears deployed at the same site and at the same time (within 2 h). Sampling gears included two beach seines (9 and 30.5 m) deployed from shore, a 14-m beach seine deployed from a boat, a 4.9-m bottom trawl, 22.9-m gillnets, and visual observations by SCUBA divers along three fixed transects (Table 1). Sampling was conducted primarily during hours of darkness. Standardized catches from the 14-m beach seine and gillnets deployed at sites 5, 6, and 7 were the only ones compared during daytime.

The catch from each gear was standardized for the amount of time the gear was fishing (hours), the size of the gear (square metres), and the number of tows or nets deployed. Units of standardized catch (number per square metre per hour) were therefore the same for both passive (gillnet) and active (trawl, seines) gears. The standardized catch (SC) for each gear was calculated as

$$SC = N \cdot A^{-1} \cdot t^{-1} \cdot n^{-1}$$

where N is the number of cod caught, A is the unit of effective fishing area of the gear (square metres) through which fish must pass to be caught, t is the time (hours) each gear was deployed, and n is the number of units deployed at one time (e.g., number of gillnets). Alternatively, n can represent the number of times a gear was deployed for a particular comparison (e.g., two trawl tows). For example, SC for a catch of 20 cod from two tows of a bottom trawl ($A = 5.5\ m^2$, Table 2) deployed for 10 min (0.17 h) each tow would be $(20/5.5\ m^2 \times 0.17\ h \times 2) = 10.67\ cod \cdot m^{-2} \cdot h^{-1}$. In all cases, A is the effective fishing area of the gear, not the horizontal area swept by the gear. Table 2 summarizes the characteristics of each gear.

Pearson product-moment correlation coefficients were calculated to determine if a linear relationship existed for catches between pairs of gears. Catches were only compared between gears that were deployed at the same site and same time. Correlations and all subsequent analyses of catch data were carried out within length groups (LG) that approximated age-classes. Length groups (estimated from Methven and Bajdik (1994) and from length frequency distributions in this study) were LG0 ≤ 96 mm SL, LG1 = 97–192 mm SL, and LG2 = 193–290 mm SL.

Differences in overall catches among gears were tested by

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Table 3. Summary of fishing effort for study of size selectivity among gears.

Gear	Months	Site	No. of times gear deployed	No. of fish measured
30.5-m seine	Sept.–Nov. 1991	1	5	153
9.0-m seine	July–Dec. 1982, 1989, 1991, 1992, 1993	1	59	945
14-m seine	Oct.–Nov. 1991	5, 6, 7	7	387
Gillnets	Aug.–Dec. 1991, July–Dec. 1993	1, 3, 4, 5, 6, 7, 8 (1991), 3 (1993)	165	3 143
4.9-m trawl	Aug.–Dec. 1991	1, 3, 4, 8	64	1 593
4.9-m trawl (rhg)	Aug.–Dec. 1992, Aug.–Dec. 1993	3, misc.	43	353
Jigger	Oct. 1991	8	1	135
25-m seine	July–Dec. 1992, July–Dec. 1993	6, 7, 34, 58	110	12 656

Note: Sites 34 and 58 are located in Trinity (48°23′N, 53°22′W) and Notre Dame (49°31′N, 54°48′W) bays, respectively. misc., 24 sites in Trinity and Conception bays; rhg, rock hopper gear.

ANOVA using the general linear model procedure of SAS (SAS Institute Inc. 1988) for each length group. ANOVA was performed on nontransformed and on $\log_{10}(SC + 1)$-transformed data. If residuals were not normal, randomization tests (Manly 1991) were conducted to determine if significant differences in catches occurred among gears. Standardized catches were randomized 400 times with gear type held constant for each test. A p-value was calculated by determining the proportion of randomizations with F-ratios greater than or equal to the observed F-ratio for each length group.

Comparison of size selectivity among gears

Data for the comparison of size selectivity among gears were mostly collected at seven sites in southern Trinity Bay from July to December each year (Table 3). Sampling gears included a 25-m beach seine, a fishing jigger, and the 4.9-m bottom trawl (modified with rock hopper gear) in addition to the gears listed previously. Comparisons of size selectivity among gears were based on sampling conducted at various times of the day or night. We recorded the method of capture for all gillnetted cod as entangled either around the mouth or around the gills and body as reported by Hovgård (1987).

Size selectivity was examined from cumulative length frequency plots for each gear by the Kolmogorov–Smirnov (K–S) test statistic d_{max} (Sokal and Rohlf 1995). In this study, d_{max} was the maximum absolute difference in the relative cumulative length frequency distributions of juvenile cod between two sampling gears. Length data were apportioned into 4-mm length-classes, i.e., the number of cod in each 4-mm length-class was determined and a cumulative length frequency made for each gear. Length-classes of 4 mm were chosen as a compromise that minimized the number of empty cells containing zero cod and maximized the total number of cells upon which comparisons were based. Multiple comparisons by the K–S tests were conducted at the adjusted α of 0.01 criteria of significance as calculated by the Dunn–Šidák method (Sokal and Rohlf 1995) for five (*i–v*) sets of planned gear comparisons: (*i*) 1 versus 5 and 7, (*ii*) 2 versus 2*, 3, 5, 6, and 6*, (*iii*) (gillnets only) 38.1- versus 25.4- and 50.8-mm meshes, (*iv*) $\text{mouth}_{38.1}$ versus $\text{gill}_{38.1}$, and (*v*) $\text{mouth}_{50.8}$ versus $\text{gill}_{50.8}$. Gear codes in *i* and *ii* are listed in Table 1. Significance criteria were adjusted to $\alpha = 0.01$ because multiple comparisons lack independence. If the outcome of a single gear comparison is significant, the outcomes of subsequent comparisons might more likely be significant as well (Sokal and Rohlf 1995). Probability values were calculated by solving eq. 11 of Miller (1956, p. 118) for the adjusted α given a known sample size and critical value of d_{max}. This equation was solved for α using only the first two terms which, depending on sample size, produced p-values accurate to two or three decimal places. This method of comparing length frequencies independent of site and year assumes that cod were randomly distributed with all length groups being equally available to all gears. The small number of shallow (<30 m) coastal sites sampled (less than nine sites for all gears except the rock hopper trawl, Table 3) and the relatively high number of tows conducted for most gears (mean >50 tows per gear type, Table 3; but note that three gears were deployed <10 times) suggest that observed differences in catches among gears were not due to a few unrepresentative catches and that this method of comparing length frequencies is appropriate.

Spatial gradients and temporal changes in catches among gears

We examined small-scale depth gradients in catches to determine if these were independent of gears. Depth gradients were calculated for the bottom trawl, SCUBA surveys, 25-m beach seine, and gillnets, all of which were deployed over a relatively wide range of depths (2.5–30 m). Spatial gradients were defined as the difference in catch at two locations relative to the separation (Schneider 1994). The vertical spatial gradient ΔC (cod per metre) was calculated as

$$\Delta C = \frac{C_{z_{i+1}} - C_{z_i}}{z_{i+1} - z_i}$$

where C_{z_i} is the mean catch at depth interval z_i and $C_{z_{i+1}}$ is the mean catch at the next depth interval. For example, a mean catch (C_{z_i}) of 10.5 fish at depth interval 10.1–12.5 m and a mean catch ($C_{z_{i+1}}$) of 22.5 fish at the next depth interval (12.6–15.0 m) yields a spatial depth gradient of $\Delta C = ((22.5 - 10.5)/2.5) = 5$ cod·m^{-1}. Spatial gradients were calculated at a resolution of 2.5 m. The vertical resolution (2.5 m) was chosen as a compromise between the number of depth classes and interpretability of the depth gradient pattern.

A further test of the relationship between depth and catch was conducted using gillnets at two coastal sites with contrasting offshore depth profiles. At site 4 near Bellevue (Table 1), bottom depth increased rapidly with distance offshore such that the depth at 400 m offshore averaged 37.3 m. This contrasts with Hant's Harbour (48°01′N, 53°16′W) in northeast Trinity Bay where the mean depth at 400 m offshore averaged 20.7 m. Seven nets formed a right-angle pattern that ran parallel to the shoreline (nets 1–3) and then away from the coast (nets 4–7). Three nets (1–3), with 100 m between each net, were set along the shore. Four additional nets (4–7), with 100 m between each net, were set in an offshore direction. Net 4, located at the junction of the longshore and cross-shore nets, was therefore common to both series of nets. Gillnets were set late in the afternoon, fished overnight, and then retrieved shortly after dawn the following day. Sampling was repeated four times (i.e., 4 days) at each site with a total of 7 nets·day^{-1} × 4 days·site^{-1} × 2 sites = 56 nets set.

We also examined small-scale temporal changes in catches to determine if day and night differences in catches were independent of gears. Site 4 was sampled eight times on 23–24 August 1993 with gillnets. Three gillnets were deployed at the same site for 3 h before being retrieved and replaced with three new nets. Site 3 was sampled on 13–15 October 1992. Two 5-min tows by the bottom trawl were conducted at 3-h intervals at this site.

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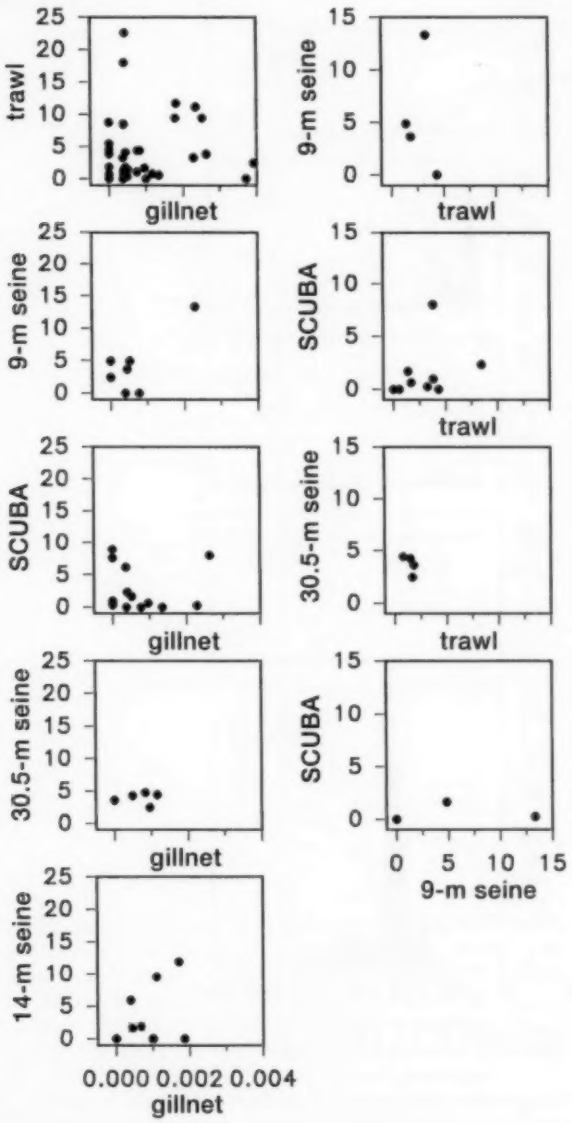
Fig. 1. Standardized catches (number·m^{-2}·h^{-1}) of LG1 cod in paired gear comparisons where gears were deployed within 2 h at the same site.



Results

Comparison of standardized catches among gears

Both the Shapiro–Wilks statistic and plots of residuals indicated that residuals were not normally distributed when standardized catches (transformed and nontransformed) were examined for significant differences among gears by ANOVA. We therefore used randomization tests (Manly 1991) on nontransformed data to test for significant differences in catches among the gears listed in Table 2. Standardized catches differed significantly among gears for each length group (LG0: $p = 0.005$, LG1: $p < 0.0001$, LG2: $p = 0.015$). Gillnet catches were orders of magnitude lower than for all other gears (Table 2).

We tested whether catches could be calibrated across gears by plotting catches of one gear against a second gear within each length group. Results for LG1 cod for all paired gear comparisons (Fig. 1) are typical for other length groups. There was only one significant correlation (out of a total of 22 comparisons): LG1 cod in gillnets were significantly correlated with LG1 cod in the 9-m beach seine ($r = 0.771$, $n = 7$, $p = 0.0446$). The lack of correlation in more than one out of 22 comparisons indicated that standardized catches could not be calibrated across gears on an absolute scale.

Comparison of size selectivity among gears

Gillnets and jiggers primarily collected individuals >150 mm SL whereas trawls and beach seines with 9-mm stretch mesh generally collected juvenile cod <200 mm SL (Fig. 2). Length frequencies from most trawls and seines contained one or two clear size modes at about 60–75 and 120–140 mm SL (Fig. 2). Consequently, many of the multiple comparisons of cumulative length frequencies among trawls and beach seines (Fig. 3) were not significantly different at the adjusted α of 0.01. For example, length frequencies of juvenile cod taken by the trawl and by the same trawl modified with rock hopper gear did not differ significantly ($d_{max} = 0.2445$, $n = 42$, $p = 0.0111$). Length frequencies among the trawl and 9- and 14-m beach seines also did not differ significantly ($d_{max} < 0.2038$, $n > 37$, $p > 0.2000$, in all cases). In general, the trawl and beach seines caught a very similar size range of juvenile cod (35–200 mm SL) with either one or two size modes being present. Cumulative length frequencies from gillnets and the fishing jigger always differed significantly from all other gears and from each other ($p < 0.0001$) because these gears generally sampled much larger cod (Figs. 2 and 3).

Three clear size modes of juvenile cod were observed in gillnet catches (Fig. 4). These were LG1 (148–190 mm SL), LG2 (190–270 mm SL), and possibly LG3 (270–370 mm SL). The individual size modes do not correspond to the three different mesh sizes (i.e., the 148–190 mm mode from the 25.4-mm mesh, the 190–270 mm mode from the 38.1-mm mesh, and the 270–370 mm mode from the 50.8-mm mesh) because the 25.4-mm mesh was ineffective at catching cod (Fig. 4) and accounted for only 36/3143 = 1.1% of the total gillnet catch. Size selectivity of gillnets appeared to be related to method of capture (gill and mouth) in addition to mesh size. The two size modes present in each of the 38.1-mm (148–190 and 205–280 mm SL) and 50.8-mm (190–250 and 250–370 mm SL) meshes correspond to method of capture, with cod being meshed around the body or gills or, alternatively, entangled near the mouth (Fig. 4). Mouth-caught cod were generally larger than gilled cod within each of these mesh sizes (Fig. 4). There were no significant differences between cumulative length frequencies of cod taken by the 25.4- and 38.1-mm meshes ($d_{max} = 0.3584$, $n = 19$, $p = 0.0119$) or between the 38.1- and 50.8-mm meshes ($d_{max} = 0.2112$, $n = 53$, $p = 0.0153$) of gillnets at the adjusted α of 0.01 (Figs. 3 and 4). Differences did occur between the 25.4- and 50.8-mm meshes ($d_{max} = 0.5728$, $n = 16$, $p < 0.0001$) as well as between gill- and mouth-caught cod taken by the 50.8-mm mesh ($d_{max} = 0.7635$, $n = 29$, $p < 0.0001$). Cumulative length frequencies of gill- and mouth-caught cod from the 38.1-mm mesh were not significantly

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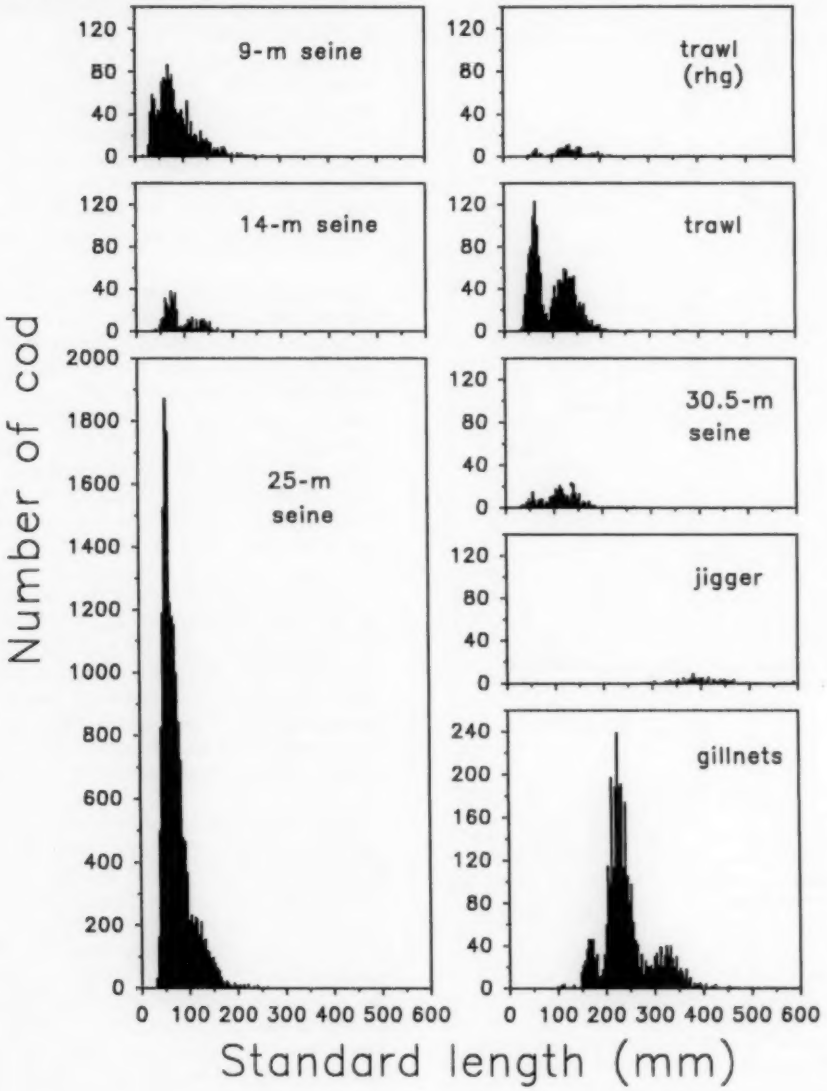
Fig. 2. Length frequency distributions of juvenile cod (4-mm length intervals) collected at several sites along the northeast coast of Newfoundland. Gears are described in the text. rhg, rock hopper gear.



different (d_{max} = 0.4966, n = 9, p = 0.0168). Very few cod <150 mm were collected by gillnets and jiggers, even though cod of this size were routinely collected by trawls and beach seines deployed in the same area at the same time. The three size modes represented in the gillnet catches (148–190, 190–270, and 270–370 mm SL) likely correspond to the upper size limit of LG1 (148–190 mm SL), LG2 (190–270 mm SL), and possibly LG3 cod (270–370 mm SL).

Spatial gradients and temporal changes in catches among gears

Spatial gradients in catches were examined to determine whether these were specific to individual gears or, alternatively, if patterns were independent of gears. Plots of catch at depth (0.1-m resolution) and of spatial depth gradients (2.5-m resolution) show that highest catches occurred at shallow depths of about 5 m for LG0, LG1, and LG2 cod taken by bottom trawl, SCUBA, 25-m beach seine, and gillnets (Fig. 5). All gear caught fewer fish at depths >27–30 m.

A further test of the relationship of catch to depth was conducted using gillnets at site 4 and at Hant's Harbour, two sites that differed in offshore depth profiles. Based on the depth-related pattern of catches described above (Fig. 5), we expected that catch would decline with increasing depth offshore. This was the pattern we observed at site 4 where depth increased from 6.7–8.3 m nearshore to 37 m at 400 m offshore (Fig. 6). At Hant's Harbour, a site with a more uniform cross-shore depth gradient (range 12.0–20.7 m, Fig. 6), cross-shore

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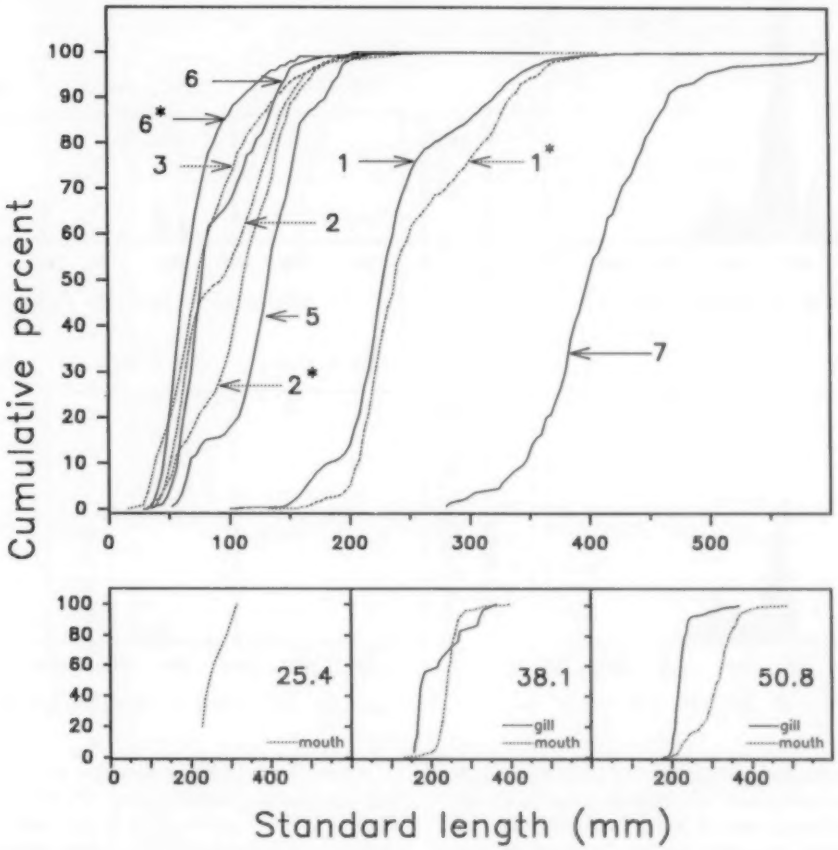
Fig. 3. Cumulative number of cod (4-mm length intervals) as a percentage. The lower panels show cumulative number of cod caught by 25.4-, 38.1-, and 50.8-mm meshes in gillnets in 1993 for each method of capture (gill, mouth). Gears: 1, all gillnet collections; 1*, all gillnet collections in 1993; 2, trawl; 2*, trawl with rock hopper gear; 3, 9-m beach seine; 5, 30.5-m beach seine; 6, 14-m beach seine; 6*, 25-m beach seine; 7, jigger.



catches of gillnetted cod were similar to longshore catches and consequently did not show the decline that was evident with depth at site 4 (Fig. 6). Catches differed significantly between longshore and cross-shore gillnets at site 4 (ANOVA, $F_{1,95} = 15.16$, $p = 0.0002$) but not at Hant's Harbour (ANOVA, $F_{1,95} = 0.83$, $p = 0.3637$), again indicating the importance of depth to the distribution of juvenile cod in the nearshore zone.

Temporal patterns in catches among gears were compared for two 24-h collections, one by bottom trawl (11–14 m, site 3) and the other by gillnets (4–17 m, site 4), to determine whether diel patterns were specific to individual gears or if patterns were independent of gears. At the temporal scale of day versus night, a strong pattern was evident with 91.6% (trawl) and 73.8% (gillnets) of all juvenile cod caught at night.

Discussion

Repeated deployment of several demersal sampling gears in different coastal habitats showed that (*i*) catches could not be calibrated across gears deployed simultaneously at the same site, (*ii*) size modes of juvenile cod were independent across gear, similar among trawls and beach seines, but contrasted with the larger cod taken by gillnets and jiggers, and (*iii*) standardized catches differed among gears, with gillnet catches being orders of magnitude lower than for all other gears. Early findings led to the formulation of additional objectives that investigated whether spatial gradients of depth and temporal changes were comparable across years. Spatial gradients and diel changes in catches were comparable across gears, with highest catches occurring close to shore in 4–7 m of water during hours of darkness.

Substantial effort was devoted in this study to matching gear by time and location to reduce error in calibration. Despite this, it proved impossible to calibrate standardized catches across gears. However, it was possible to identify a series of length modes that were consistent across most gears. Modes occurred at about 50–77, 120–140, and approximately, 200–300 mm SL. The smallest mode, best sampled by beach seines and trawls with 9-mm mesh, was age 0 cod that settled in autumn (Pinsent and Methven 1997). Cod between 200–300 mm were best sampled by gillnets and were in the size range (22–27 cm) of 2-year-olds (Fleming 1960). The size mode in between age 0 and age 2 cod (≈120–140 mm SL) likely represents age 1 cod that have overwintered, but there

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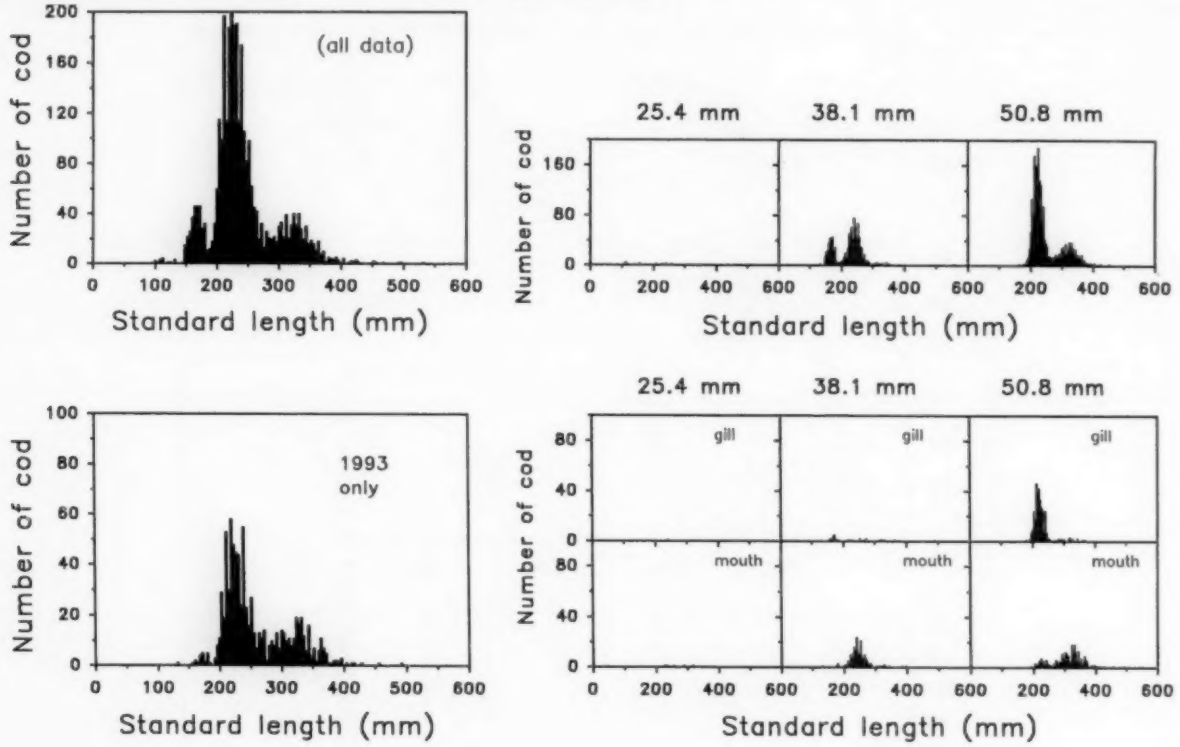
Fig. 4. Length frequency distributions of juvenile cod (4-mm intervals) collected by gillnets (upper panels) in 1991–1993 with corresponding breakdown by stretch mesh size (25.4, 38.1, 50.8 mm). Lower panels show length frequency distributions of all cod taken by gillnets in 1993 with corresponding breakdown by mesh size and method of capture (gill, mouth).



appears to be no confirmation of this for cod from Newfoundland based on ages determined from otoliths. Caution should be taken when assigning ages to individual gillnetted cod based solely on length frequency modes. Peaks in the size distributions of gillnetted cod are not only influenced by mesh size selection but are also related to the way cod were meshed (gill or mouth). Thus, it is important to distinguish between the two smallest size modes (50–77 and 120–140 mm SL) sampled by small-mesh trawls and seines that apparently correspond to the size distribution of the population and the larger mode (200–300 mm) caused by the mesh selection of the gillnets.

Patterns of relative change in abundance with time of day and with depth could be identified independently of gear type. The different types of gear (passive, active, and visual observations by divers) used to sample juvenile cod over a 24-h period at the same site in this and other studies (Keats 1990; Methven and Bajdik 1994; Gibson et al. 1996) all show higher catches at night, indicating that this pattern is independent of gear and characteristic of coastal populations of LG0 and LG1 cod. We interpret this pattern to be due more to an inshore movement at dusk or night than to a substantial change in catchability (Methven and Bajdik 1994; Gibson et al. 1996). Rapid inshore and offshore movements at dusk and dawn by a variety of fishes (Helfman 1993) indicate that collections taken at these times may not be representative of typical daytime densities.

Spatial depth gradients were also similar across gears when averaged across sampling sites. Highest catches occurred at shallow (4–7 m) depths close to the coast. This pattern is not unique to LG0 and LG1 cod in Newfoundland waters. Catches of 0-group cod off the English and Welsh coasts taken by a 2-m beam trawl were highest at about 6 m (Riley and Parnell 1984). Highest catches of age-1 cod sampled by gillnets off southwestern Greenland were taken at 3–10 m. Catches were lowest at depths <3 m and >20 m (Hansen and Lehmann 1986; Hovgård and Nygaard 1990). Gibson et al. (1996) reported that highest catches of juvenile cod in Scotland occurred at 5 m over the range 0.5–5.0 m. Acoustic surveys in Finnmark, northern Norway, showed that most juvenile cod occurred at depths <35 m, with highest densities occurring closest to the coast where the vessel could not sample (Olsen and Soldal 1989). These studies, conducted across a variety of habitats, depths, and gears, indicate that the coastal distribution of 0-group cod occurs at shallow depths and that larger juveniles occur at progressively deeper depths and distance from the coast (Hansen 1966; Hislop 1984; Riley and Parnell 1984; Tremblay and Sinclair 1985; Dalley and Anderson 1997). This positive relationship between size and depth is characteristic of many species and implies an ontogenetic movement towards deeper water with increasing size (Macpherson and Duarte 1991). This was first described by Heincke (1913) for plaice (*Pleuronectes platessa*) and was referred to as Heincke's Law (Wimpenny 1953). Relative to the adult stages,

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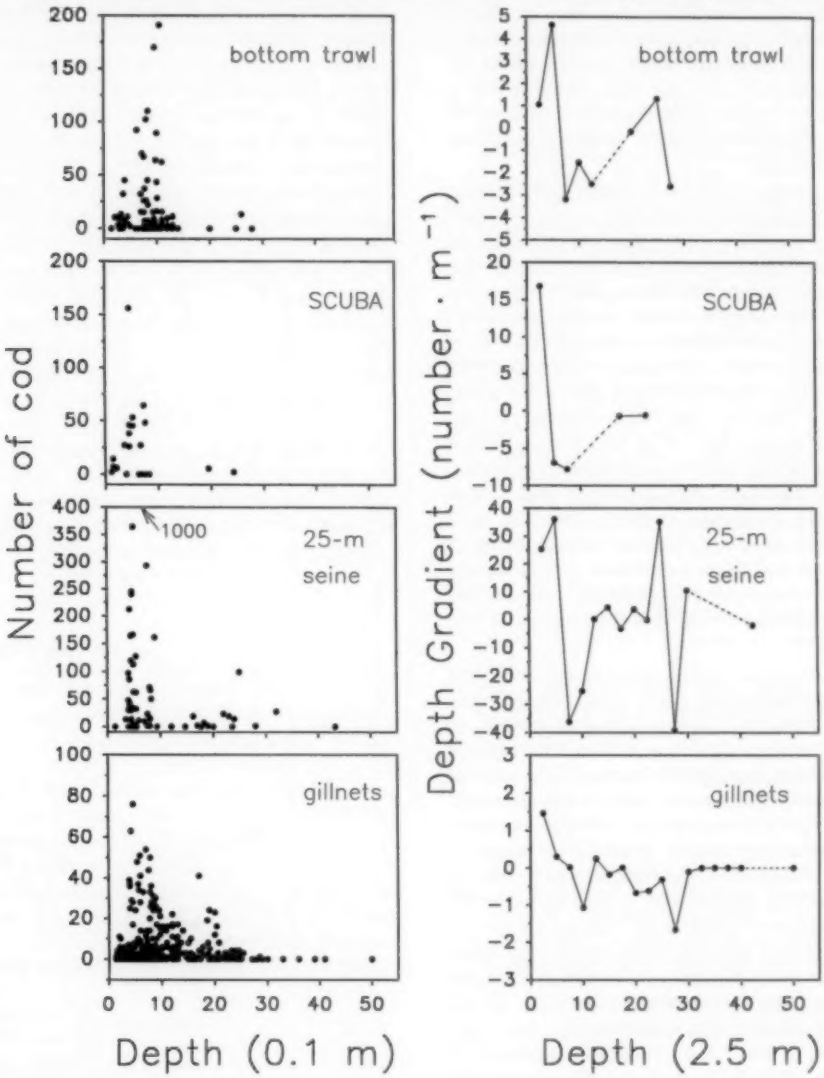
Fig. 5. Number of cod in relation to depth (0.1-m resolution) and depth gradients (2.5-m resolution). Depth gradients are defined in the text.



larvae and juveniles of many temperate demersal fish species occur in shallow and hence relatively well-lighted water.

At a scale of hundreds of kilometres, LG0 and LG1 cod are presently (mid-1990s) confined to the coast of Newfoundland during autumn (Dalley and Anderson 1997). Our study extends this result to a finer scale of tens of metres within the coastal zone where LG0 and LG1 cod reached maximum densities at depths of 4–7 m. This confirms observations of Lear and Green (1984) that nursery areas for LG0 cod are located along the coast. The prevailing southward flow of the Labrador Current will tend to carry eggs and larvae toward the coast due to Coriolis forces, although this tendency is episodically reversed at the surface by strong wind events from the southwest (Templeman 1966; Frank and Leggett 1982; Rose and Leggett 1988; Schneider and Methven 1988; Ings et al. 1997*a*). A physical model of egg and larval drift (Helbig et al. 1992) showed that eggs spawned offshore generally remained offshore, but more recent models (Davidson and deYoung 1995; Pepin and Helbig 1997) showed that coastal transport was possible for particles seeded along the shelf break to the north but not to the east of Newfoundland. These observations, together with the current absence of LG0 cod away from the coast (Dalley and Anderson 1997), a spawning failure of the offshore components of the 2J3KL Newfoundland–Labrador cod stock (Dalley and Anderson 1997), and well-documented spawning along the northeast coast of Newfoundland (Thompson 1943; Hutchings et al. 1993; Laprise and Pepin 1995; Smedbol and Wroblewski 1997), are consistent with a coastal origin for many of the newly settled cod collected along the coast in shallow (4–7 m) water. In the past, coastal areas may have served as nursery areas for both inshore and offshore spawning fish (Lear and Green 1984). Concentration of newly settled

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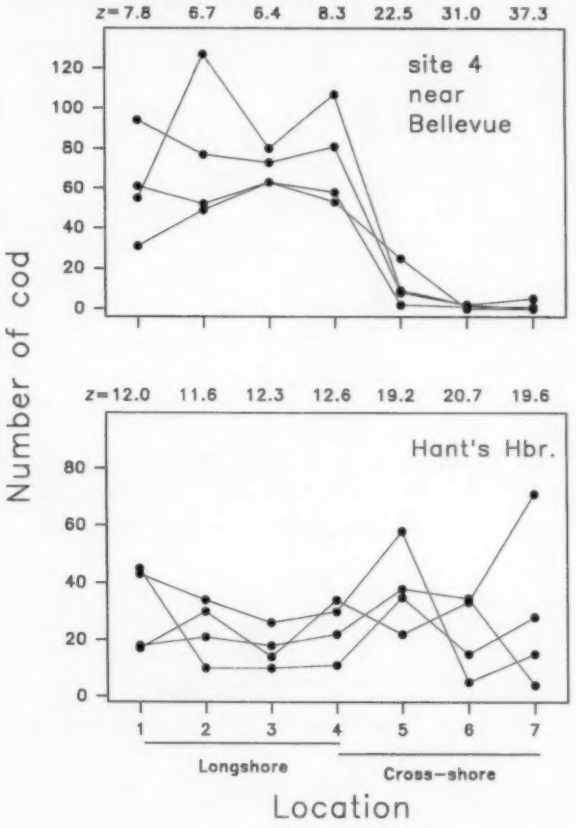
demersal cod in the horizontal dimension can be achieved either by (*i*) an active migration towards the coast, possibly in response to depth, and factors that covary with depth such as light, salinity, or food gradients (Riley and Parnell 1984; Tremblay and Sinclair 1985; Heessen 1991; Angel 1992) or (*ii*) from wind-induced coastal upwelling where demersal juveniles can be moved toward the coast in bottom water drawn shoreward during upwelling.

To explain this pattern of vertical distribution, we propose that shallow waters act as traps for vertically migrating pelagic cod that settle upon encounter with suitable bottom habitat and that undergo increasingly extensive vertical migration as they increase in size before settling. Vertical migration begins during the pelagic stage, as juveniles ascend towards the surface during darkness and descend during daylight (Koeller et al. 1986; Perry and Neilson 1988). On Georges Bank, these diel vertical migrations kept cod in contact with their pelagic prey (*Neomysis americana*, *Tisbe* sp., and *Pagurus* larvae) at thermally stratified and nonstratified sites (Perry and Neilson 1988). As the length of individual cod increases, the vertical extent of the pelagic migration increases (Perry and Neilson 1988) until individuals eventually encounter the bottom. A positive relationship between length of cod and the extent of diel vertical migration is reported for another gadid, walleye pollock (*Theragra chalcogramma*, Bailey 1989), and for fish in general (Neilson and Perry 1990). This trapping mechanism is testable.

Predictions are that (*i*) size of individual cod at settlement will be less on shallow banks and coastal areas than on deeper banks, (*ii*) shallow sites will have a higher proportion of smaller cod than deeper sites, and (*iii*) recently settled cod will be more aggregated than their pelagic counterparts because shallow banks (and especially coastal areas) act as traps that concentrate settled cod. This trapping mechanism is consistent with ultimate, or evolutionary, factors favouring settlement of juvenile cod in coastal habitats. These factors include reduced predation and maintaining contact with a familiar and relatively abundant pelagic food supply. Both factors increase survival. Predation is reduced because larger (predatory) fishes tend to occupy deeper water (Helfman 1978; Macpherson and Duarte 1991). Coastal sites also provide abundant fleshy macroalgae, a preferred habitat that, in addition to cobble, provides juvenile cod with cover from predation (Keats et al. 1987; Gotceitas et al. 1995). Settlement in shallow water also helps maintain contact with pelagic food in the surface layer until cod reach 60–100 mm, the size at which they make the transition to predominately benthic prey (Lomond et al. 1998).

The high densities observed in shallow water contrast with the distribution of newly settled cod off Nova Scotia and New England where LG0 and LG1 cod were either not collected in shallow water or attained maximum densities at depths greater than the 4–7 m observed in this study (Targett and McCleave 1974; McCleave and Fried 1975; Macdonald et al. 1984; Horne and Campana 1989; Lough et al. 1989; Black and Miller 1991; Hanson 1996; but see Tupper and Boutilier 1995). Water temperature may be an important variable that restricts 0- and 1-group cod to deeper water south of Newfoundland and in Norway where in the southern Gulf of St. Lawrence, age 0 cod are absent at depths <10 m (Hanson 1996) and along the Skagerrak coast of Norway, age 1 cod occur in deeper water during summer when subsurface temperatures are too warm

Fig. 6. Number of cod collected by individual gillnets set about 100 m apart in a line along the shore (locations 1–4) and in a line in an offshore direction (locations 4–7) at two sites (upper and lower panels) with contrasting offshore depth profiles. Mean depth (*z*, m) of four gillnets is indicated immediately above each panel over the longshore and cross-shore location to which it refers. Seven gillnets, one at each location, were set overnight on each of four occasions (i.e., four lines of data) for each site in August 1992. The seven gillnets set at any one time for each site formed a right-angle shaped pattern, with the gillnet at location 4 being common to both the longshore series and the cross-shore series of nets.



(Danielssen and Gjøsæter 1994). A second possibility relates to spawning locations south of Newfoundland. If spawning occurs primarily offshore and passive eggs and larvae are not advected towards the coast, then extensive settlement may not occur at the coast. For example, similarity in the patterns of egg and larval distributions offshore on the Scotian Shelf at any one time, as well as the persistence of the larval distributions over certain offshore banks led O'Boyle et al. (1984) to suggest that eggs and larvae were retained by gyral circulation associated with offshore banks and that the spawning and nursery grounds are often located within the same geographical area offshore (Gagné and O'Boyle 1984).

At present (1992 onward), the coastal zone nursery area for LG0 cod is the only confirmed source of recruits in Newfoundland. Our study, in conjunction with Dalley and Anderson (1997), establishes that shallow coastal depths represent the

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centre, and not the edge, of the distribution of LG0 cod off eastern Newfoundland. These results indicate that a coastal survey (e.g., Schneider et al. 1997; Ings et al. 1997*b*) together with an inshore–offshore survey (e.g., Dalley and Anderson 1997) in deeper water are required to track annual changes in distribution and abundance of juvenile cod off eastern Newfoundland during the 3 years prior to recruitment to the fishery. Each survey has disadvantages. Coastal surveys with bottom-sampling seines do not sample large (>200 mm) juvenile cod well, likely because of gear avoidance and the preference for deeper water (Gregory and Anderson 1997). Coastal surveys (e.g., Tveite 1984; Ings et al. 1997*b*) are also restricted to relatively smooth bottom habitats near the coast. Consequently, they may not be a good indicator of cod abundance in deeper water. Offshore demersal surveys conducted from large ships (e.g., Dalley and Anderson 1997) cannot sample the immediate nearshore zone where density of LG0 cod was highest at 4–7 m. In addition, offshore surveys generally do not catch as many 0-group cod compared with 1-group cod, due possibly to no sampling near the coast. Neither survey by itself can accurately represent the abundance and distribution of juvenile cod. Both a coastal survey and an offshore survey are required to track relative cohort strength of demersal cod during the first 3 years of life.

Acknowledgments

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References

Angel, M.V. 1992. Long-term, large scale patterns in marine pelagic systems. *In* Aquatic ecology: scale, pattern, and process. *Edited by* P.S. Giller, A.G. Hildrew, and D.G. Raffaelli. Blackford Scientific Publications, London, U.K. pp. 403–439.

Bailey, K.M. 1989. Interaction between the vertical distribution of juvenile walleye pollock *Theragra chalcogramma* in the eastern Bering Sea, and cannibalism. Mar. Ecol. Prog. Ser. **53**: 205–213.

Black, R., and Miller, R.J. 1991. Use of the intertidal zone by fish in Nova Scotia. Environ. Biol. Fishes, **31**: 109–121.

Cushing, D.H. 1981. Fisheries biology — a study in population dynamics. 2nd ed. University of Wisconsin Press, Madison, Wis.

Dalley, E.L., and Anderson, J.T. 1997. Age-dependent distribution of demersal juvenile Atlantic cod (*Gadus morhua*) in inshore/offshore northeast Newfoundland. Can. J. Fish. Aquat. Sci. **54**(Suppl. 1): 168–176.

Danielssen, D.S., and Gjøsæter, J. 1994. Release of 0-group cod, *Gadus morhua* L., on the southern coast of Norway in the years 1986–1989. Aquat. Fish. Manage. **25**(Suppl. 1): 129–142.

Davidson, F.J.M., and deYoung, B. 1995. Modelling advection of cod eggs and larvae on the Newfoundland Shelf. Fish. Oceanogr. **4**: 33–51.

Fleming, A.M. 1960. Age, growth and sexual maturity of cod (*Gadus morhua* L.) in the Newfoundland area, 1947–1950. J. Fish. Res. Board Can. **17**: 775–809.

Frank, K.T., and Leggett, W.C. 1982. Coastal water mass replacement: its effects on zooplankton dynamics and the predator–prey complex associated with larval capelin (*Mallotus villosus*). Can. J. Fish. Aquat. Sci. **39**: 991–1003.

Gagné, J.A., and O'Boyle, R.N. 1984. The timing of cod spawning on the Scotian Shelf. *In* The propagation of cod *Gadus morhua* L. *Edited by* E. Dahl, D.S. Danielssen, E. Moksness, and P. Solemdal. Flødevigen Rapp. **1**(Part 1): 501–517.

Gibson, R.N., Robb, L., Burrows, M.T., and Ansell, A.D. 1996. Tidal, diel and longer term changes in the distribution of fishes on a Scottish sandy beach. Mar. Ecol. Prog. Ser. **130**: 1–17.

Godø, O.R., Gjøsæter, J., Sunnanå, K., and Dagesund, O. 1989. Spatial distribution of 0-group gadoids of mid-Norway. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **191**: 273–280.

Gotceitas, V., Fraser, S., and Brown, J.A. 1995. Habitat use by juvenile Atlantic cod (*Gadus morhua*) in the presence of an actively foraging and non-foraging predator. Mar. Biol. **123**: 421–430.

Gregory, R.S., and Anderson, J.T. 1997. Substrate selection and use of protective cover by juvenile Atlantic cod *Gadus morhua* in inshore waters of Newfoundland. Mar. Ecol. Prog. Ser. **146**: 9–20.

Gunderson, D.R. 1993. Surveys of fisheries resources. John Wiley & Sons, Inc., Toronto, Ont.

Hansen, P. 1966. Cod: its biology and habitat. *In* Géo-Économie de la morue. *Edited by* J. Malaurie. Mouton and Company, Paris. pp. 287–314.

Hansen, H.H., and Lehmann, K.M. 1986. Distribution of young cod in coastal regions of west Greenland, 1985. NAFO SCR. Doc. 86/42 Ser. No. N1158.

Hanson, J.M. 1996. Seasonal distribution of juvenile Atlantic cod in the southern Gulf of St. Lawrence. J. Fish Biol. **49**: 1138–1152.

Harden Jones, J.R. 1968. Fish migration. Arnold, London, U.K.

Hayes, M.L. 1989. Active fish capture methods. *In* Fisheries techniques. *Edited by* L.A. Nielsen and D.L. Johnson. American Fisheries Society, Bethesda, Md. pp. 123–145.

Heessen, H.J.L. 1991. The distribution of cod in the North Sea. NAFO SCR Doc. 91/109 Ser. No. N2002.

Heincke, F. 1913. Investigations on the plaice. 1. The plaice fishery and protective regulations. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **17**: 1–153.

Helbig, J., Mertz, G., and Pepin, P. 1992. Environmental influences on the recruitment of Newfoundland/Labrador cod. Fish. Oceanogr. **1**: 39–56.

Helfman, G.S. 1978. Patterns of community structure in fishes: summary and overview. Environ. Biol. Fishes, **3**: 129–148.

Helfman, G.S. 1993. Fish behaviour by day night and twilight. *In* Behaviour of teleost fishes. *Edited by* T.J. Pitcher. Chapman and Hall, London, U.K. pp. 479–512.

Hislop, J.R.G. 1984. A comparison of the reproductive tactics and strategies of cod, haddock, whiting and Norway pout in the North Sea. *In* Fish reproduction: strategies and tactics. *Edited by* G.W. Potts and R.J. Wootton. Academic Press, London, U.K. pp. 311–329.

Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **20**: 1–228.

Hjort, J. 1926. Fluctuations in the year-classes of important food fishes. J. Cons. Cons. Int. Explor. Mer, **1**: 1–38.

Horne, J.K., and Campana, S.E. 1989. Environmental factors influencing the distribution of juvenile groundfish in nearshore habitats of southwestern Nova Scotia. Can. J. Fish. Aquat. Sci. **46**: 1277–1286.

Hovgård, H. 1987. Effects of gill net selection on survey results in the

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Greenland young cod survey. NAFO SCR Doc. 87/28 Ser. No. N1312.

Hovgård, H.H., and Nygaard, K.H. 1990. Young cod distribution and abundance in west Greenland inshore areas, 1989. NAFO SCR. Doc. 90/30 Ser. No. N1747.

Hubert, W.A. 1989. Passive capture techniques. *In* Fisheries techniques. *Edited by* L.A. Nielsen and D.L. Johnson. American Fisheries Society, Bethesda, Md. pp. 95–122.

Hutchings, J.A., Myers, R.A., and Lilly, G.R. 1993. Geographical variation in the spawning of Atlantic cod, *Gadus morhua*, in the northwest Atlantic. Can. J. Fish. Aquat. Sci. **50**: 2457–2467.

Ings, D.W., Horne, J.K., and Schneider, D.C. 1997*a*. Influence of episodic upwelling on capelin (*Mallotus villosus*) and Atlantic cod (*Gadus morhua*) catches in Newfoundland coastal waters. Fish. Oceanogr. **6**: 41–48.

Ings, D.W., Schneider, D.C., and Methven, D.A. 1997*b*. Detection of a recruitment signal in juvenile Atlantic cod (*Gadus morhua*) in coastal nursery areas. Can. J. Fish. Aquat. Sci. **54**(Suppl. 1): 25–29.

Keats, D.W. 1990. A nocturnal inshore movement of juvenile cod *Gadus morhua* L. in eastern Newfoundland. J. Exp. Mar. Biol. Ecol. **139**: 167–173.

Keats, D.W., South, G.R., and Steele, D.H. 1987. The role of macroalgae in the distribution and feeding of juvenile cod (*Gadus morhua* L.) in inshore waters of eastern Newfoundland. Can. J. Zool. **65**: 49–53.

Koeller, P.A., Hurley, P.C.F., Perley, P., and Neilson, J.D. 1986. Juvenile fish surveys on the Scotian Shelf: implications for year-class assessments. J. Cons. Cons. Int. Explor. Mer, **43**: 59–76.

Laprise, R., and Pepin, P. 1995. Factors influencing the spatio-temporal occurrence of fish eggs and larvae in a northern, physically dynamic coastal environment. Mar. Ecol. Prog. Ser. **122**: 73–92.

Lear, W.H., and Green, J.M. 1984. Migration of the northern Atlantic cod and the mechanism involved. *In* Mechanisms of migration in fishes. *Edited by* J.D. McCleave, G.P. Arnold, J.J. Dodson, and W.W. Niel. Plenum Press, New York. pp. 309–315.

Lear, W.H., Fleming, A.M., and Wells, R. 1980. Results of small cod surveys in eastern Newfoundland during 1959–64. NAFO SCR Doc. 80/IX/144 Ser. No. N0218.

Lincoln, R.J., Boxshall, G.A., and Clark, P.F. 1982. A dictionary of ecology, evolution and systematics. Cambridge University Press, Cambridge, U.K.

Lomond, T.M., Schneider, D.C., and Methven, D.A. 1998. The transition from pelagic to benthic prey of 0–1 group Atlantic cod. Fish. Bull. U.S. In press.

Lough, R.G., Valentine, P.C., Potter, D.C., Auditore, P.J., Bolz, G.R., Neilson, J.D., and Perry, R.I. 1989. Ecology and distribution of juvenile cod and haddock in relation to sediment type and bottom currents on eastern Georges Bank. Mar. Ecol. Prog. Ser. **56**: 1–12.

Macdonald, J.S., Dadswell, M.J., Appy, R.G., Melvin, G.D., and Methven, D.A. 1984. Fishes, fish assemblages, and their seasonal movements in the lower Bay of Fundy and Passamaquoddy Bay, Canada. Fish. Bull. U.S. **82**: 121–139.

Macpherson, E., and Duarte, C.M. 1991. Bathymetric trends in demersal fish size: is there a general relationship. Mar. Ecol. Prog. Ser. **71**: 103–112.

Manly, B.F.J. 1991. Randomization and Monte Carlo methods in biology. Chapman and Hall, London, U.K.

May, R.C. 1974. Larval mortality in marine fishes and the critical period concept. *In* The Early Life History of Fish, the Proceedings of an International Symposium held at the Dunstaffnage Marine Research Laboratory of the Scottish Marine Biological Association at Oban, Scotland. *Edited by* J.H.S. Blaxter. Springer-Verlag, Berlin. pp. 3–19.

McCleave, J.D., and Fried, S.M. 1975. Nighttime catches of fishes in a tidal cove in Montsweag Bay near Wiscasset Maine. Trans. Am. Fish. Soc. **104**: 30–34.

Methven, D.A., and Bajdik, C. 1994. Temporal variation in size and abundance of juvenile Atlantic cod (*Gadus morhua*) at an inshore site off eastern Newfoundland. Can. J. Fish. Aquat. Sci. **51**: 78–90.

Miller, L.H. 1956. Table of percentage points of Kolmogorov statistics. Biometrics, **51**: 111–121.

Neilson, J.D., and Perry, R.I. 1990. Diel vertical migrations of marine fishes: an obligate or facultative process? *In* Advances in marine biology. Vol. 26. *Edited by* J.H.S. Blaxter and A.J. Southward. Academic Press, London, U.K. pp. 115–168.

O'Boyle, R.N., Sinclair, M., Conover, R.J., Mann, K.H., and Kohler, A.C. 1984. Temporal and spatial distribution of ichthyoplankton communities on the Scotian Shelf in relation to biological, hydrological, and physiographic features. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **183**: 27–40.

Olsen, S., and Soldal, A.V. 1989. Observations on inshore distribution and behaviour of 0-group northeast Arctic cod. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **191**: 296–302.

Pepin, P., and Helbig, J.A. 1997. Distribution and drift of Atlantic cod (*Gadus morhua*) eggs and larvae on the northeast Newfoundland shelf. Can. J. Fish. Aquat. Sci. **54**: 670–685.

Perry, R.I., and Neilson, J.D. 1988. Vertical distributions and trophic interactions of age-0 Atlantic cod and haddock in mixed and stratified waters of Georges Bank. Mar. Ecol. Prog. Ser. **49**: 199–214.

Peterman, R.M., Bradford, M.J., Lo, N.C.H., and Methot, R.D. 1988. Contribution of early life stages to interannual variability in recruitment of northern Anchovy (*Engraulis mordax*). Can. J. Fish. Aquat. Sci. **45**: 8–16.

Pinsent, D.L., and Methven, D.A. 1997. Protracted spawning of Atlantic cod (*Gadus morhua*) in Newfoundland waters: evidence from otolith microstructure. Can. J. Fish. Aquat. Sci. **54**(Suppl. 1): 19–24.

Potter, D.C., Lough, R.G., Perry, R.I., and Neilson, J.D. 1990. Comparison of the MOCNESS and IYGPT pelagic samplers for the capture of 0-group cod (*Gadus morhua*) on Georges Bank. J. Cons. Cons. Int. Explor. Mer, **46**: 121–128.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. No. 191.

Riley, J.D., and Parnell, W.G. 1984. The distribution of young cod. *In* The propagation of cod *Gadus morhua* L. *Edited by* E. Dahl, D.S. Danielssen, E. Moksness, and P. Solemdal. Flødevigen Rapp. **1**(Part 2): 563–580.

Rose, G.A., and Leggett, W.C. 1988. Atmosphere–ocean coupling in the northern Gulf of St. Lawrence: effects of wind forced variation in sea temperatures on currents and nearshore distributions and catch rates of *Gadus morhua*. Can. J. Fish. Aquat. Sci. **45**: 1234–1243.

SAS Institute Inc. 1988. SAS/STAT users guide, release 6.03 edition. SAS Institute Inc., Cary, N.C.

Schnack, D. 1973. On the reliability of methods for quantitative surveys of fish larvae. *In* The Early Life History of Fish, the Proceedings of an International Symposium held at the Dunstaffnage Marine Research Laboratory of the Scottish Marine Biological Association at Oban, Scotland. *Edited by* J.H.S. Blaxter. Springer-Verlag, Berlin. pp. 201–211.

Schneider, D.C. 1994. Quantitative ecology: spatial and temporal scaling. Academic Press, Toronto, Ont.

Schneider, D.C., and Methven, D.A. 1988. Response of capelin to wind-induced thermal events in the southern Labrador Current. J. Mar. Res. **46**: 105–118.

Schneider, D.C., Methven, D.A., and Dalley, E.L. 1997. Geographic contraction in juvenile fish: a test with northern cod (*Gadus morhua*) at low abundances. Can. J. Fish. Aquat. Sci. **54**(Suppl. 1): 187–199.

Sette, O.E. 1943. Biology of the Atlantic mackerel (*Scomber scombrus*) of North America. Part I. Early life history, including

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growth, drift, and mortality of the egg and larval populations. U.S. Fish Wildl. Serv. Fish. Bull. **50**: 149–237.

Sissenwine, M.P. 1984. Why do fish populations vary? *In* Exploitation of marine communities. *Edited by* R.M. May. Dahlem Workshop Reports. Life Sci. Res. Rep. **32**: 59–94.

Smedbol, R.K., and Wroblewski, J.S. 1997. Evidence for inshore spawning of northern Atlantic cod (*Gadus morhua*) in Trinity Bay, Newfoundland, 1991–1993. Can. J. Fish. Aquat. Sci. **54**(Suppl. 1): 177–186.

Sokal, R.R., and Rohlf, F.J. 1995. Biometry. The principles and practice of statistics in biological research. 3rd ed. W.H. Freeman and Company, New York.

Solemdal, P., and Ellertsen, B. 1984. Sampling fish larvae with large pumps: quantitative and qualitative comparisons with traditional gear. *In* The propagation of cod, *Gadus morhua*. *Edited by* E. Dahl, D.S. Danielssen, E. Moksness, and P. Solemdal. Flødevigen Rapp. **1**(Part 1): 335–363.

Steele, D.H. 1983. Marine ecology and zoogeography. *In* Biogeography and ecology of the Island of Newfoundland. *Edited by* G.R. South. Junk Publishers, The Hague, The Netherlands. pp. 421–465.

Suthers, I.M., and Frank, K.T. 1989. Inter-annual distributions of larval and pelagic juvenile cod (*Gadus morhua*) in southwestern Nova Scotia determined with two different gear types. Can. J. Fish. Aquat. Sci. **46**: 591–602.

Targett, T.E., and McCleave, J.D. 1974. Summer abundance of fishes in a Maine tidal cove with special reference to temperature. Trans. Am. Fish. Soc. **103**: 325–330.

Templeman, W. 1966. Marine resources of Newfoundland. Bull. Fish. Res. Board Can. No. 154.

Thompson, H. 1943. A biological and economic study of cod (*Gadus collarias*, L.) in the coastal waters of west Iceland. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **191**: 264–272.

Tremblay, M.J., and Sinclair, M. 1985. Gulf of St. Lawrence cod: age-specific geographic distributions and environmental occurrences from 1971 to 1981. Can. Tech. Rep. Fish. Aquat. Sci. No. 1387.

Tupper, M., and Boutilier, R.G. 1995. Effects of habitat on settlement, growth and postsettlement survival of Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **52**: 1834–1841.

Tveite, S. 1984. 0-Group cod investigations along the Norwegian Skagerrak coast. *In* The propagation of cod, *Gadus morhua*. *Edited by* E. Dahl, D.S. Danielssen, E. Moksness, and P. Solemdal. Flødevigen Rapp. **1**(Part 2): 581–590.

Wimpenny, R.S. 1953. The plaice. Edward Arnold and Co., London, U.K.

Appendix. Description of sampling gears

Beach seines

9-m seine

The 9-m by 1.5-m-deep beach seine with 9-mm stretch mesh and its method of deployment are described in Methven and Bajdik (1994).

14-m seine

The 14-m beach seine was constructed of 15-mm stretch mesh with a codend liner of 9-mm stretch mesh. This seine sinks to the bottom and sampled from the bottom to about 1.5–2.0 m above the bottom. It did not sample from the surface to the bottom as did the 9- and 30.5-m seines. The 14-m seine was deployed by boat to a distance of 55 m offshore and was hauled towards shore by towing lines. Retrieval of the 14- and 25-m beach seines is described in Lear et al. (1980).

25-m seine

Specifications and deployment of the 25-m beach seine are described in Schneider et al. (1997).

30.5-m seine

The 30.5-m by 2.4-m-deep beach seine had a 2.4-m^3 collection bag and was constructed entirely of 9-mm stretch mesh. One person remained onshore holding a pole attached to the end of the seine while the other end was taken offshore by a person wearing chest waders. This seine was fished in one arclike sweep such that an area of about a quarter of a circle was sampled.

Bottom trawl

The trawl was a 4.9-m semiballoon bottom trawl with a 5.2-m headrope and a 6.4-m footrope. The footrope was fitted with eight 7.6 × 12.7 cm rollers spaced evenly with 69-cm centres between which hung with one loop of galvanized chain. The mesh in the wings, top, belly, and codend was 32–38 mm stretch with a 9-mm stretch mesh liner in the codend. Thread size was No. 12 in the body and No. 18 in the codend. Chaffing gear of 63.5-mm stretch mesh was attached to the underside of the net and codend. Trawl doors were made of wood with metal runners and measured 76 cm long by 38 cm deep. Each door weighed about 7 kg. The amount of towing warp was three to four times the water depth. Tows were usually limited to 5–10 min each at a speed of 2.5–3.0 $km \cdot h^{-1}$. The foot gear of the trawl was modified to include rock hopper gear (see Gunderson 1993) in 1992 and 1993. This consisted of groups of four 7.5-cm-diameter rubber discs that were evenly spaced every 10.2 cm by metal spacers. The net was attached to a 4-mm-diameter wire (that ran through the discs to prevent them from rolling) by three links of chain. Each link of chain was 25 mm long, thus ensuring that the space between the rock hopper gear and the net was minimized.

SCUBA

SCUBA surveys were conducted by divers after dusk along rope transects that were anchored to the bottom. Transects started in shallow water close to shore and extended offshore for 61 m (site 1), 118 m (site 3), and 113 m (site 4). The start and finish depths were 1.7–4.4 m (site 1), 6.9–10.0 m (site 3), and 4.5–14.5 m (site 4). All cod observed within 3 m of either side of the transect and within about 1.5 m of the bottom were counted. Visibility at night depended on the dive site but usually exceeded 4 m with an underwater light. Divers recorded all information on plastic slates. Five underwater transects were conducted by divers who recorded cod on underwater video (H18 mm camcorder, Sony model V101, enclosed in an Amphibico housing with two 50-W lights). Juvenile cod did not appear to be either attracted to or repulsed by divers (see Keats et al. 1987; Keats 1990) or underwater lights.

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Gillnets

Gillnets were 22.9 m by 2.4 m deep and contained three 7.6-m panels, each of different size mesh (25.4-, 38.1-, and 50.8-mm stretch mesh). The floatline was made of foamcore, a flexible styrofoam core running through the centre of a 9.5-mm nylon rope. The footline was 6.4-mm-diameter lead line that was attached to building bricks, as weights, at each end of the net. Meshes were made of No. 69 monofilament line (0.28 mm thick). Gillnets were set perpendicular to the coast in a line from shallow to deep water (sites 3 and 4) or along the shore (sites 1, 6, and 7) so as not to interfere with boat traffic. Nets were usually set shortly before dusk and were retrieved by 08:00–10:00 the next day. Soak time was about 15 h.

Jigger

The fishing jigger is known locally as a Norwegian-style jigger and is manufactured by Sølvkroken. It is silver in colour, 21 cm long, weighs 498 g, and has a single treble hook with red plastic around the shaft.

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Monitoring organic pollution and eutrophication in the Grand River, Ontario, by means of diatoms

Eugen Rott, Hamish C. Duthie, and Eveline Pipp

Abstract: Diatom analysis discriminates between the impacts on river water quality of treated urban wastewaters and diffuse nutrient sources from farmland. Evaluation of organic pollution and trophic levels in the Grand River, Ontario, using two diatom indices shows a clear differentiation among 10 sampling sites over a distance of 214 km. Sites in the central reaches that are influenced by both urban discharges and agricultural runoff have the lowest water quality. The ranking of sites according to both diatom indices is consistently independent of substratum and seasonality. Ordination of samples by multivariate analysis results in a primary separation of the spring and summer communities and a secondary separation of upper, central, and lower reaches. Substratum differences are only apparent at the tertiary level, and mainly for midsummer samples from the upper reaches. Canonical correspondence analysis shows that the largest portion of the observed variability in species composition can be explained by a seasonal gradient related to temperature and by longitudinal gradients of nitrate-nitrogen, conductivity, and chloride. Differences in species composition between nutrient-rich sites and polluted sites are identified. Compared with a study conducted in the 1960s, the Grand River shows clear signs of increased eutrophication.

Résumé : L'analyse des diatomées permet de distinguer entre les incidences, sur la qualité de l'eau des cours d'eau, des eaux usées urbaines traitées et des matières nutritives d'origine agricole de source diffuse. l'évaluation par les diatomées de la pollution organique et des niveaux trophiques dans la rivière Grand, en Ontario, montre L'existence de différences nettes entre dix sites d'échantillonnage répartis sur une distance de 214 km. La qualité de l'eau des sites du centre qui subissent l'influence des rejets urbains et des eaux de ruissellement agricoles est la moins bonne. Le classement des sites en fonction des deux indices des diatomées est, de façon constante, indépendant du substrat et de la saison. L'ordination des échantillons par analyse multivariée permet d'établir une distinction entre les communautés de printemps et d'été et, ensuite, entre les tronçons de l'amont, du centre et de l'aval. Les écarts entre les substrats n apparaissent qu au troisième niveau, et surtout pour les échantillons du tronçon supérieur prélevés au milieu de l'été. L'analyse de correspondance canonique montre que la plus grande partie de la variabilité observée au sein de la composition spécifique peut être expliquée par un gradient saisonnier lié à la température et par des gradients longitudinaux de l'azote nitrate, de la conductivité et du chlorure. Les écarts de la composition spécifique entre les sites riches en matières nutritives et les sites pollués sont présentés. Si l'on se fonde sur les résultats d'une étude réalisée au cours des années 1960, la rivière Grand présente des signes apparents d'eutrophisation accrue. [Traduit par la Rédaction]

Introduction

The use of diatoms for river monitoring has an especially long tradition in the United States (Patrick 1949). However, multivariate analytical approaches and applications in North America date back only a few years (see Charles 1996). In recent years, it has become more and more evident that benthic algae in general (e.g., Whitton and Rott 1996) and epilithic diatoms in particular are useful for monitoring changes in river water quality (Cox 1991; Round 1993). The reason for using diatoms for bioassessment is that living diatoms occur throughout all river habitats and react specifically and quickly to inorganic nutrient enrichment (eutrophication). Some diatoms are also known to be capable of taking up and using organic substances (e.g., Hellebust and Lewin 1977; van Dam et al. 1994) and thus to be active components of the self-purification process in wastewater treatment and surface waters (see Rott et al. 1997).

Nowadays, many lowland rivers suffer from eutrophication from diffuse sources by fertilizer runoff from agricultural areas and from point-source discharges of organic wastewaters from urban areas. The Grand River is a case in point for studying these parallel effects, since the cities are concentrated in the central part of the catchment area whereas the intensively cultivated land extends mainly from the middle to the lowest reaches. This was the background to earlier investigations of the benthic and planktonic diatom flora of the Grand River (Fraser 1966; Sreenivasa and Duthie 1973).

Diatom analysis is proposed as a valuable diagnostic tool for quantifying stream ecosystem conditions in Canada in the sense of Kilgour et al. (1996). In recent years the methodological tools for bioassessment have improved and permit the present investigation to test the hypotheses that (*i*) diatoms allow simultaneous monitoring of both biodegradable organic pollution and eutrophication, (*ii*) the results for both criteria differ, and (*iii*) the result is not dependent on (*a*) substratum type and (*b*) season. The main objective here is not to create a new method in addition to the many existing diatom indices (see Whitton and Kelly 1995), but to test the effectiveness of easily applied practical methods such as the differentiating species method of Lange-Bertalot (1979) for pollution and a

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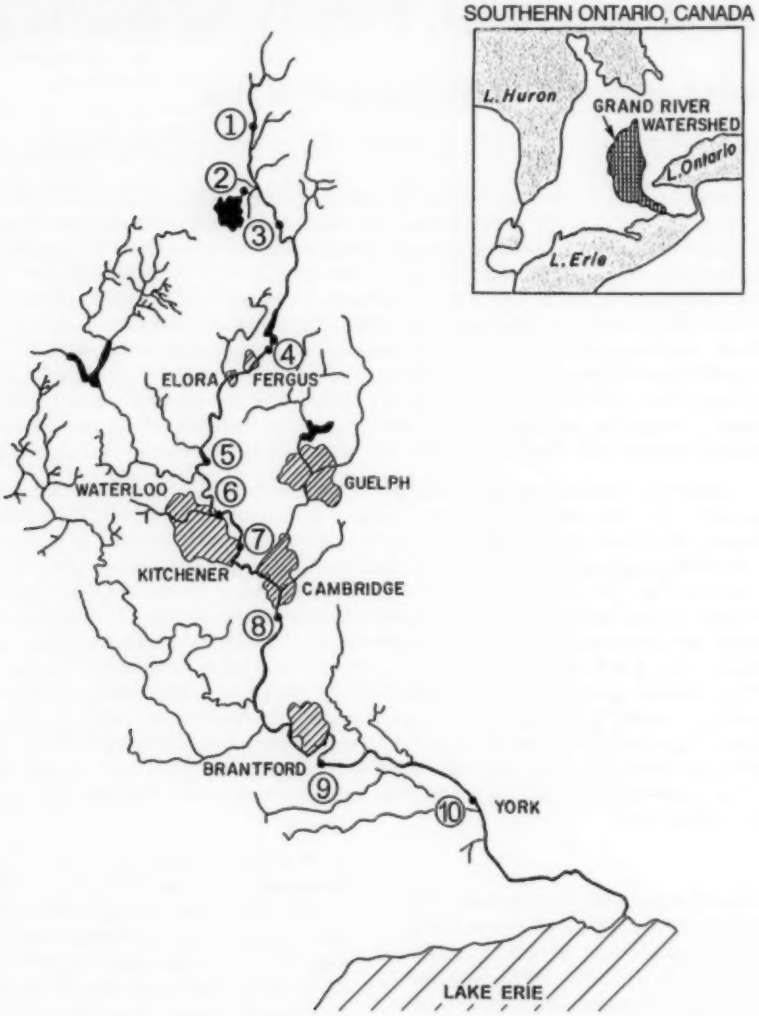
Fig. 1. Geographic location of the Grand River and location of sampling sites described in the text. 1, Keldon; 2, Luther; 3, 10th line; 4, Belwood; 5, Conestogo; 6, Bridgeport; 7, Freeport; 8, Galt; 9, Newport; 10, York.



preliminary approach to a trophic evaluation of river sites based on the indicator species list of van Dam et al. (1994). In addition, numerical analysis of the diatom and environmental data identifies the most important regulating environmental variables and probable causes for the observed diatom distribution patterns.

Materials and methods

Site descriptions

The Grand River drains an area of 6965 km^2 in southern Ontario, Canada, and has a population of over 670 000 people. It originates 20 km south of Georgian Bay at an elevation of 526 m above sea level and flows over length of 298 km to its mouth on Lake Erie at 355 m above sea level. The basin is dominated by silt and clay tills overlaying permeable limestone, but kame and outwash sand and gravel deposits are common (GRCA 1982). To adequately represent the broad spectrum of environments along the river valley, 10 sections of the river (Fig. 1, sites 1 and 3–10) including one major upstream tributary (Fig. 1, site 2) were sampled. The sites cover the river 30 km from the source to 44 km above the mouth.

The sites can be characterized as follows.

(1) Keldon — the river passes under a highway; a few submerged macrophytes; water clear, brown colored by humic substances; nondiatom periphyton very diverse, e.g., with species of the genera *Chara*, *Rivularia*, and *Chaetophora*;

(2) Luther — at inflow of tributary from Luther Marsh at a road bridge; flow highly variable; runoff by manipulation of a dam; open site, unshaded by trees; slightly turbid water;

(3) 10th Line Bridge — situated north from Grand Valley on the right shore (west) 30 m above the bridge over a major highway; at this place, flow is reduced due to a rock dam downstream; brown-colored, slightly turbid water; rich emergent macrophyte vegetation near shore;

(4) Belwood — right shore area 20 m up from the first bridge crossing the river below the dam; fast-flowing stretch; channel covered mainly by stone plates;

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Table 1. Important physicochemical variables in the Grand River for characterizing the main sections obtained from sample ordination (see Fig. 2) from April to August 1994 and comparison with data in Fraser (1966).

		Sites 3 and 4		Sites 5–10	
	Year	April–June	July, August	April, May	June–August
Temperature (°C)	1994	3.9–11.2	16.7–22.2	3.5–22.3	21.4–28.0
pH	1966	7.8–8.1	7.2–8.1	8.0–8.7	7.6–8.5
	1994	8.0–8.5	7.9–8.3	8.1–8.7	8.2–8.8
Conductivity ($\mu S \cdot cm^{-1}$)	1966	280–380	190–410	180–**530**	200–**540**
	1994	333–454	294–434	485–754	449–767
	Median	414	409	667	668
Alkalinity (mequiv.·L^{-1})	1994	3.7–4.4	2.8–3.8	3.8–4.4	3.5–4.7
Chemical oxygen demand ($mg \cdot L^{-1}$)	1994	24.8–27.8	25.1–28.9	14.1–23.4	19.8–29.2
	Median	26.3	25.1	16.8	24.3
Oxygen saturation (%)	1994	95–119	71–106	91–**181**	51–**173**
Chloride ($mg \cdot L^{-1}$)	1994	8.7–13.2	7.7–11.5	21.3–85.0	17.2–83.9
	Median	10.7	10.6	56.5	58.9
NH_4-N ($\mu g \cdot L^{-1}$)	1994	22–140	2–110	2–120	6–118
	Median	31	62	40	38
NO_3-N ($\mu g \cdot L^{-1}$)	1966	50–180	210–290	100–**630**	100–**640**[a]
	1994	485–1860	10–755	1830–4060	635–3770
	Median	940	280	2750	1500
NO_2-N ($\mu g \cdot L^{-1}$)	1994	9–22	4–66	10–**172**	9–95
	Median	13	22	38	20
PO_4-P ($\mu g \cdot L^{-1}$)	1994	2–19	1–2	2–95	1–66
	Median	11	1.5	10	7
Total phosphorus ($\mu g \cdot L^{-1}$)	1966	20–50	20–50	10–**230**	10–**370**
	1994	7–48	22–44	22–**194**	20–**142**
	Median	22	32	52	60
Turbidity (units·L^{-1})	1994	1.3–10.2	3.1–7.9	1.1–35.9	1.8–23.2
	Median	3.3	4.4	2.6	6.2

Note: Values are ranges and medians where indicated; significantly higher maxima are in bold type.
[a]Singular peak value of 2770 $\mu g \cdot L^{-1}$.

(5) Conestogo — right shore upstream of a highway bridge; stone surfaces covered by calcified algae (e.g., *Homoeothrix crustacea*); poor periphyton crop; clear water; fast flow;
(6) Bridgeport — right shore 100 m upstream the bridge, near the mouth of the polluted and slightly foamy Laurel Creek; generally turbid water; fast flow;
(7) Freeport — downstream right shore below bridge of old Highway 8; shallow side arm with island formation; medium flow; gravel; slightly turbid water;
(8) Galt — situated left shore 50 m down from the first bridge downstream the wastewater treatment plant; water turbid and foamy on all occasions, sometimes black; rich macroalgal crop of *Cladophora*; fast flow;
(9) Newport — situated 100 m upstream of a highway bridge on the right shore; muddy turbid water, green to brownish; rich riverine vegetation;
(10) York — situated at village center park on left shore side; rich macrophyte vegetation; slow to intermediate flow; highly turbid water.

Sampling

Periphyton was sampled on two consecutive days monthly from April to August 1994, as close as possible to the dates of water sampling. In addition, four samples from October 1993 were analysed. From each station, periphyton sampling consisted of three replicates of scrapes from the upper surface of a stone, mixed and kept separately. In addition, two samples from dead leaves of submerged grass, present in all except three stations, were sampled from April to July.

Water chemistry samples were taken adjacent to the phytobenthos samples by the Grand River Conservation Authority, Cambridge, Ont., and analysed by the Water Quality Branch of the Ontario Ministry of the Environment and Energy. The detailed methodology is given in MOE (1981). However, Keldon (station 1) and Luther (station 2) were not sampled. The data set included all major physical and chemical variables including chemical oxygen demand and nutrients (Table 1). Biochemical oxygen demand data could not be used due to implausibly low and scattered values, probably caused by delays of >2 days between sampling and analysis.

Diatom procedures

Diatom samples were cleaned in the laboratory by boiling in H_2O_2 for 15–30 min and three replicates of each sample of cleaned material were mounted in Naphrax. For further details of methodologies including identification from light and electron microscopy, see Rott (1995).

Altogether, 100 samples were counted. From the epilithic samples, the slide with the best dispersion of cleaned frustules was selected. A total of 300 individuals per sample were counted under oil immersion at 1000× magnification. For three stations from the different river sections for June and August, three parallel epilithic samples were analysed. The relative proportions of the species in the total count were calculated. For statistical evaluation, species in quantities below 1% or occurring in less than five samples were neglected.

Data analysis

Information on the sensitivity of the species towards organic pollution is given in Table 2 and is based on the differentiating species concept of Lange-Bertalot (1979). Species classification follows Krammer

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Table 2. Species list of the 59 frequent diatoms in the Grand River (abundance ≥1% in at least five samples), frequency (*F*) and maximum relative abundance (*A*) in all 100 samples, sensitivity towards organic pollution (S),[a] and trophic state indicator value (*T*).[b]

Abbreviation	Species	*F*	*A*	S	*T*
ACHN DELI	*Achnanthes delicatula* (Kützing) Grunow	6	3	t*	—
ACHN LANC	*Achnanthes lanceolata* (Brébisson) Grunow	21	5	t	5
ACHN JACK	*Achnanthes minutissima* Kützing var. *jackii* (Rabenhorst) Lange-Bertalot	13	45	s	—
ACHN MINU	*Achnanthes minutissima* Kützing var. *minutissima*	88	81	s	7
ACHN SAPR	*Achnanthes minutissima* Kützing var. *saprophila* Kobayashi & Mayama	5	14	ht	—
AMPI PELL	*Amphipleura pellucida* (Kützing) Kützing	25	8	s*	2
AMPH LIBY	*Amphora libyca* Ehrenberg	65	21	s	—
COCC PEDI	*Cocconeis pediculus* Ehrenberg	65	56	t*	5
COCC PLAC	*Cocconeis placentula* Ehrenberg	54	61	t	5
CYCL MENE	*Cyclotella meneghiniana* Kützing	27	30	t	5
CYMB AFFI	*Cymbella affinis* Kützing	20	17	s	5
CYMB AMPH	*Cymbella amphicephala* Nägeli	7	5	s*	2
CYMB CAES	*Cymbella caespitosa* (Kützing) Burn	9	9	t*	7
CYMB SILE	*Cymbella silesiaca* Bleisch	56	7	s	7
CYMB SINU	*Cymbella sinuata* Gregory	7	2	s	3
DIAT MONI	*Diatoma moniliformis* Kützing	8	21	t*	—
DIAT TENU	*Diatoma tenuis* Agardh	30	21	t	5
DIAT VULG	*Diatoma vulgaris* Bory	25	16	t*	4
FRAG MESO	*Fragilaria capucina* Desmazières var. *mesolepta* (Rabenhorst) Rabenhorst	6	6	s*	—
FRAG VAUC	*Fragilaria capucina* Desmazières var. *vaucheriae* (Kützing) Lange-Bertalot	53	42	t–ht	5
FRAG PINN	*Fragilaria pinnata* Ehrenberg	30	10	s	7
FRAG ULNA	*Fragilaria ulna* (Nitzsch) Lange-Bertalot	36	62	t–ht	7
FRAG ACUS	*Fragilaria ulna* (Nitzsch) Lange-Bertalot var. *acus* (Kützing) Lange-Bertalot	12	4	t	5
GOMP MINU	*Gomphonema olivaceum* (Hornemann) Brébisson var. *minutissimum* Hustedt	10	31	s	2
GOMP OLIV	*Gomphonema olivaceum* (Hornemann) Brébisson var. *olivaceum*	59	70	s	3
GOMP PARV	*Gomphonema parvulum* (Kützing) Kützing var. *parvulum*	43	14	ht	5
GOMP SAPR	*Gomphonema parvulum* (Kützing) Kützing var. *saprophilum* Lange-Bertalot & Reichardt	8	19	ht	6
MERI CIRC	*Meridion circulare* (Gréville) Agardh	21	33	t*	7
NAVI ATOM	*Navicula atomus* (Kützing) Grunow	20	18	ht	6
NAVI CAPR	*Navicula capitatoradiata* Germain	65	17	t	5
NAVI CRCE	*Navicula cryptocephala* Kützing	19	5	t	7
NAVI CRTE	*Navicula cryptotenella* Lange-Bertalot	85	32	t	7
NAVI GREG	*Navicula gregaria* Donkin	40	7	t	5
NAVI LANC	*Navicula lanceolata* (Agardh) Ehrenberg	45	75	t	5
NAVI MINI	*Navicula minima* Grunow	15	24	ht	5
NAVI RADI	*Navicula radiosa* Kützing	12	7	s*	4
NAVI REIC	*Navicula reichardtiana* Lange-Bertalot	73	13	t*	—
NAVI SAPR	*Navicula saprophila* Lange-Bertalot & Bonik	11	12	ht	5
NAVI TRIP	*Navicula tripunctata* (O.F.Müller) Bory	69	22	t	5
NAVI TRIV	*Navicula trivialis* Lange-Bertalot	10	10	t	5
NITZ ACIC	*Nitzschia acicularis* (Kützing) W. Smith	11	3	t*	5
NITZ ARCH	*Nitzschia archibaldi* Lange-Bertalot	14	3	t*	5
NITZ DISS	*Nitzschia dissipata* (Kützing) Grunow	88	40	t	4
NITZ FONT	*Nitzschia fonticola* Grunow non sensu Hustedt	9	2	s	4
NITZ FRUS	*Nitzschia frustulum* (Kützing) Grunow	15	7	t	5
NITZ GFOR	*Nitzschia graciliformis* Lange-Bertalot & Simonsen	14	30	t*	5
NITZ GLIS	*Nitzschia gracilis* Hantzsch	16	6	s*	3
NITZ HEUF	*Nitzschia heufleriana* Grunow	17	2	t*	—
NITZ INCT	*Nitzschia incognita* Legler & Krasske non Krasske	7	3	—	—
NITZ INCO	*Nitzschia inconspicua* Grunow	13	10	t*	5
NITZ LACU	*Nitzschia lacuum* Lange-Bertalot	5	5	s*	3
NITZ LINE	*Nitzschia linearis* (Agardh) W. Smith	10	5	t*	4
NITZ PALE	*Nitzschia palea* (Kützing) W. Smith	71	27	ht	6
NITZ RECT	*Nitzschia recta* Hantzsch	34	8	s	7
NITZ SOCI	*Nitzschia sociabilis* Hustedt	30	7	t	5

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Table 2 (*concluded*).

Abbreviation	Species	*F*	*A*	S	*T*
RHOI ABBR	*Rhoicosphenia abbreviata* (Agardh) Lange-Bertalot	43	33	t	5
STEP HANT	*Stephanodiscus hantzschii* Grunow	5	4	t*	6
STEP MINU	*Stephanodiscus minutulus* (Kützing) Cleve & Möller	16	15	s	6
SURI BREB	*Surirella brebissonii* Krammer & Lange-Bertalot	25	9	t	—

[a]According to Lange-Bertalot (from Krammer and Lange-Bertalot 1986): s, sensitive; t, tolerant; t–ht, moderately to highly tolerant; ht, highly tolerant; *modified after first author's observations.

[b]Following van Dam et al. (1994): 2, oligotraphentic to mesotraphentic; 3, mesotraphentic; 4, mesotraphentic to eutraphentic; 5, eutraphentic; 6, hypereutraphentic; 7, oligotraphentic to eutraphentic.

and Lange-Bertalot (1986) developed for large rivers in Germany. For some species the classification was modified due to the first author's experience (marked by asterisks in Table 2). The trophic indicator values in Table 2 were taken from van Dam et al. (1994), who integrated qualitative classifications of the species from the literature into a six-grade scale with grade 7 being assigned to eurytraphentic (=indifferent) species.

Saprobic water quality classes were assigned using percentages of sensitive, tolerant, and highly tolerant species according to Krammer and Lange-Bertalot (1986, p. 61). Trophic indices of the samples are arithmetic means of the indicator values of the species according to van Dam et al. (1994), weighted by their relative abundance. The eurytraphentic species were excluded from calculations, since they occur over a broad range of nutrient conditions and therefore are not good indicators.

To describe similarities of sampling sites and sampling occasions in terms of benthic diatom species composition, the data on relative abundance of the species in the 100 samples were subjected to numerical analysis. The sample and species groups shown in Figs. 2 and 3, respectively, were obtained by means of TWINSPAN (Hill 1979). Relative abundances were transformed into four pseudospecies classes: <5, 6–15, 16–50, and >50%.

Correlations of species composition and abiotic characteristics of the samples were evaluated for 45 samples with the most complete data set of environmental variables using the multivariate statistical package CANOCO (ter Braak 1988). Relative abundances of species were used without transformation. From the physicochemical variables (Table 1), alkalinity was excluded because of its high colinearity with pH and conductivity, and chemical oxygen demand and NO_2 were excluded because they were only available for a small portion of the data set. Oxygen saturation was split into the variables "oversaturation" (saturation–100, 0 in undersaturated samples) and "undersaturation" (100–saturation, 0 in oversaturated samples). Substratum type was split into two nominal variables, "PHYT" (0 for stone samples, 1 for grass samples) and "LITH" (complementary to PHYT).

Results and discussion

Water quality

The size of the river expressed by stream order according to Strahler (1957) increases significantly between the highest and lowest sites. The clearwater sites in the more pristine upper part rank into stream order 2–4, the middle part with highly variable turbidity into stream order 4–5, and the lower part with high silt load into stream order 5–6. For the lowermost sections near site 8 the discharge varies from 20 $m^3 \cdot s^{-1}$ in summer and autumn to peak values of up to 500 $m^3 \cdot s^{-1}$ during snowmelt in spring or during thunderstorms in autumn. The hydraulic regime of the river is managed by dam regulation of a natural lake (Luther Marsh, upstream site 2, Fig. 1) and a large reservoir (Belwood, upstream site 4, Fig. 1), both situated in the upper part of the catchment, so that during low-water periods the runoff is enhanced.

The winter ice and snow cover of the river and the reduced runoff in summer cause a large annual variation in temperature (Table 1). The water of the river is well buffered and alkaline. Compared with the criteria for unpolluted situations and the threshold values for drinking water given in Chapman (1996, p. 77 ff.), the nutrient levels in the Grand River are low to moderate for orthophosphate, moderate to high for total phosphorus, moderate for ammonia, but frequently high for nitrate-nitrogen and chloride. The maxima of the nutrient components are well within the limits for eutrophic situations (which are generally higher for running waters than for lakes), but chloride concentrations at and downstream of Freeport exceed the maximum tolerable concentration given in the European Union standard for drinking water (Chapman 1996, p. 80).

There are some indications in our data set that pulses of nutrients occur after heavy rains in autumn and during snowmelt in spring. Especially in the upper sections (down to Conestogo), nutrient peaks parallel high turbidity in several cases. These effects are considered within a recent nutrient export coefficient model described for two tributaries of the Grand River (Kilgour et al. 1996; Winter and Duthie 1997). There is a clear increase in nitrogen compounds from the middle part of the river downstream, caused most probably by runoff from intensively cultivated areas, since the wastewater treatment in the densely populated areas includes in most cases phosphorus elimination, in one case (city of Guelph) ammonia stripping as well (Mason et al. 1989). The comparison of 1994 with data from the early 1960s (Table 1) shows that progressing eutrophication is mainly evident from an increase in nitrates in the lower river sections (down from site 5, Conestogo); however, some peak values were also high earlier.

Situations of high phosphate and nitrate concentrations are normally accompanied by oxygen oversaturation, while turbid and ammonia-rich waters tend to be undersaturated. Oxygen oversaturation measured during the day is most probably caused by oxygen production by periphyton and macrophytes and oxygen consumption processes by community respiration. A strong decrease in oxygen during the night was recorded in the later 1980s (Mason et al. 1989), and in summer 1994, minima below 4 $mg \cdot L^{-1}$ were measured during night (D. Fellows, Grand River Conservation Authority, personal communication). In some areas (e.g., site 8, Galt), backwater pools with black reduced sediments were observed during summer sampling.

Diatom and environmental analyses

Of the total of 138 species found in the river (Rott 1995), 59

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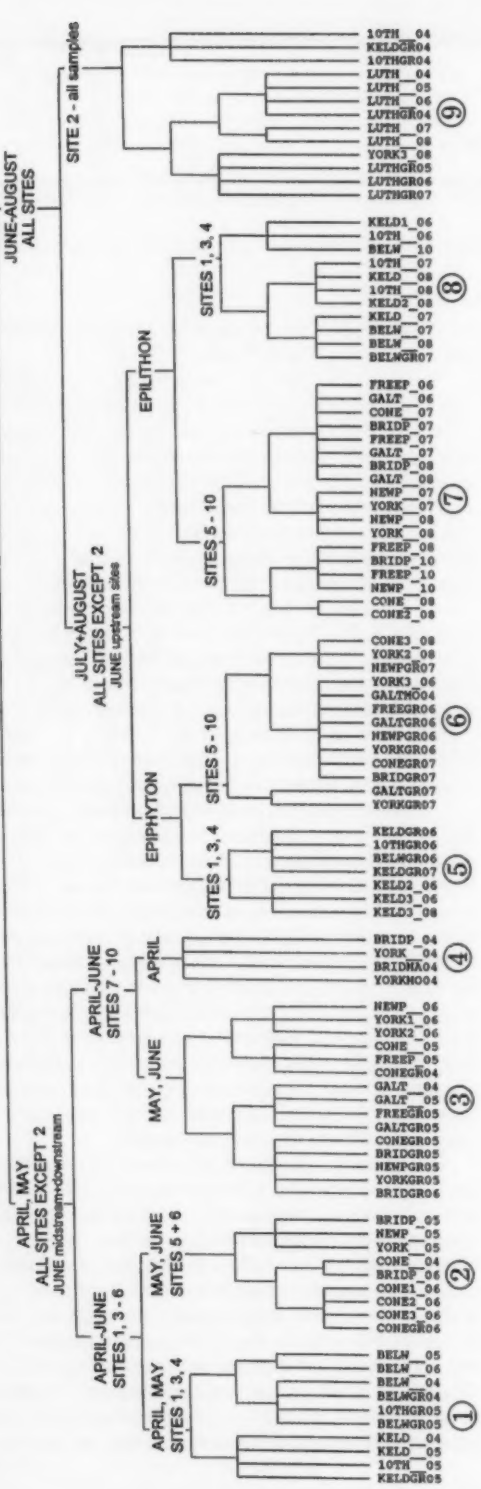

Fig. 2. Ordination of samples according to TWINSPAN. See Fig. 3 for average relative abundance of the frequent species and major indicator species. For abbreviations of the sites, the first four letters were used followed by substrate type (_, stone; GR, grass; MA, macrophyte; MO, moss) and month of sampling.

are included in the numerical analysis and are used to analyse substratum differences and spatiotemporal variability. The majority of the latter species (Table 2) are common representatives of lowland running waters, except for a few components from oligotrophic streams (e.g., *Gomphonema olivaceum* var. *minutissimum*) and from the plankton of larger rivers (mainly *Cyclotella meneghiniana*). In addition to many elements of the epilithic flora, mainly comprising species of the genera *Achnanthes*, *Cymbella*, *Diatoma*, *Fragilaria*, and *Gomphonema*, components of the overlaying silt flora (sensu Round1993) such as *Navicula lanceolata*, *Surirella brébissonii*, and several species of the genus *Nitzschia* are common.

According to the differentiating species concept of Lange-Bertalot (1979) the majority of the 59 species — and among them almost all of the frequent and dominant species — are pollution tolerant (32) or pollution sensitive (17). Only two species, which tolerate more than moderate pollution, *Fragilaria ulna* and *Fragilaria capucina* var. *vaucheriae*, were abundant in the upstream sections in April and May. The seven highly tolerant species (tolerating or preferring highly polluted conditions) were constantly present in the lowermost river sections with highest proportions in July and August, but relative abundances were generally below 5%.

The largest portion of the taxa (23) are indicators of eutrophic conditions. With the exception of *Gomphonema olivaceum* and *Gomphonema olivaceum* var. *minutissimum*, all oligotraphentic to mesotraphentic species are species with maximum relative abundances <5%. Eutraphentic to hypertraphentic species were rare as well, with the exception of *Nitzschia palea* (maximum relative abundance 27%), *Navicula atomus* (18%), and *Stephanodiscus minutulus* (15%) (see Table 2). Among the eurytraphentic species, *Achnanthes minutissima* var. *minutissima*, *Navicula cryptotenella*, and *Fragilaria ulna* reach high abundances. The 10 taxa not classified by van Dam et al. (1994) mostly are varieties or species that have been described recently and therefore are not yet quoted in the literature with respect to their ecological preferences.

The saprobic ranking of the species along the differentiating species concept of Lange-Bertalot (Table 2) is in many cases paralleled by trophic status ranks derived from van Dam et al. (1994). Frequently, pollution-sensitive taxa correspond to the oligotraphentic and mesotraphentic categories whereas pollution-tolerant taxa parallel the eutraphentic and hypertraphentic classes with few exceptions. One example is *Cymbella affinis*, a taxon comprising two distinctly different ecomorphs, an oligotraphentic and a eutraphentic one (Hofmann 1994).

The grouping of sites and seasonal aspects obtained from TWINSPAN ordination (Fig. 2) separated primarily the spring aspect from the summer aspect, independent from substrata and sites with the exception of site 2, the outflow of Luther Marsh. For this site, all samples from all dates and substrata were classified together (group 9, Fig. 2) and separated at the second level from the summer samples of the other sites. The secondary separation of the spring samples is found between the upstream and midstream sites 1 and 3–6 and the lowermost sites 7–10. In spring (April–June) the samples for the midstream sites 5 and 6 (group 2) are separated from sites 1, 3, and 4, but ranked closer to the samples of the uppermost sections. In July and August the midstream sites are more similar to sites 7–10. Within the downstream sites the April aspect (group 4)

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differs from May and June samples (group 3). In summer (June–August), differences in substratum (epiphyton (groups 5 and 6) versus epilithon (groups 7 and 8)) become evident, but these differences were more significant in the upper river sites 1, 3, and 4 (groups 5 and 8, Fig. 2) than in sites 5–10.

The ordination of the common diatoms showing co-occurrence of species according to TWINSPAN (Fig. 3, left side) separates primarily two well-defined seasonal aspects with *Gomphonema olivaceum*, *Navicula lanceolata*, and *Surirella brébissonii* dominating in spring and *Achnanthes minutissima* dominating in summer. *Cocconeis placentula* and *Cocconeis pediculus* occur especially in samples from grasses and mosses. Whereas many of these species were present in almost all river sections in different relative proportions from site to site, some species are restricted to parts of the river: e.g., *Navicula lanceolata* and *Rhoicosphenia abbreviata* are exclusively occurring in the middle and lower sections, and *Gomphonema olivaceum* var. *minutissimum*, *Achnanthes minutissima* var. *jackii*, and other rare oligotraphentic species (see Rott 1995) only occur in the uppermost river sites. *Fragilaria ulna* showed a peak in the uppermost river sections in spring and was rare at all other places.

The seasonal changes in dominant species follow from *Diatoma* in October 1993 to *Gomphonema olivaceum* var. *olivaceum* in April, *Navicula lanceolata* in May, *Cocconeis pediculus* in June, and *Cocconeis placentula* together with *Cyclotella meneghiniana* in July. These changes can be reidentified in the TWINSPAN results. However, longitudinal differences persist over the seasons.

According to the canonical correspondence analysis (Figs. 4 and 5), the largest portion of the variance in assemblage composition can be explained by a seasonal gradient (DATE, $r^2 = 0.9$) related to temperature ($r^2 = 0.95$) and by longitudinal gradients (SITE, $r^2 = 0.78$) related to conductivity ($r^2 = 0.75$), nitrate-nitrogen ($r^2 = 0.73$), and chloride ($r^2 = 0.70$). Correlations with total phosphorus, oxygen oversaturation, and turbidity are weaker; those with orthophosphate, nitrate, and oxygen undersaturation are not significant. Situations of elevated phosphate and nitrate concentrations are related to oxygen oversaturation, while turbid and ammonia-rich waters tend to be undersaturated. Eigenvalues and correlation coefficients between species composition and environmental variables are high for both axis 1 (0.51 and 0.96, respectively) and axis 2 (0.39 and 0.93, respectively) and show that the data set is well structured.

The samples are mainly ordinated along a temperature gradient parallel to the *x*-axis (Fig. 4), with May samples located at the right side of the graph, June samples near the origin, and July and August samples at the left side. Figure 4 also shows clear longitudinal gradients for each month and for samples from both substrata. In May and June the longitudinal differences in species composition are most related to a strong nitrate gradient close to the second axis of the ordination whereas temperatures were almost the same at all sites (11–13 and 18–21°C, respectively). In July and August the longitudinal gradients are parallel to the *y*-axis from the uppermost to the midstream sites (increase in nitrate) and parallel to the *x*-axis from the midstream to the downstream sites (increase in water temperature and total phosphorus). Thus the temperature gradient is a gradient both of sampling date and of location along the river. Other variables increasing downstream at all dates,

Fig. 3. Ordination of 59 selected species (abundance ≥1%, present in at least five samples) according to TWINSPAN and average relative abundance in the nine sample groups displayed in Fig. 2. Major indicator species (according to TWINSPAN) and their highest abundances are boxed. See Table 2 for species abbreviations.

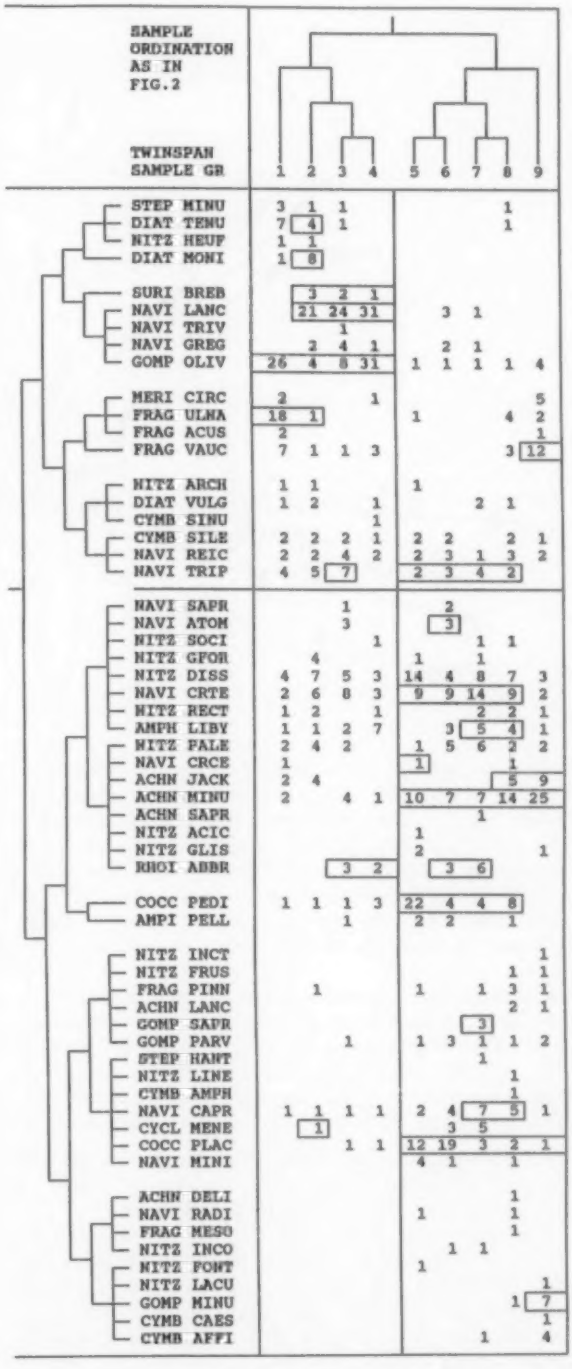
SAMPLE ORDINATION AS IN FIG.2
TWINSPAN SAMPLE GR
1 2 3 4 5 6 7 8 9
STEP MINU 3 1 1 1
DIAT TEMU 7 4 1 1
NITZ HEUP 1 1
DIAT MONI 1 8
SURI BREB 3 2 1
NAVI LANC 21 24 31 3 1
NAVI TRIV 1
NAVI GREG 2 4 1 2 1
GOMP OLIV 26 4 8 31 1 1 1 1 4
MERI CIRC 2 1 5
FRAG ULNA 18 1 1 4 2
FRAG ACUS 2 1
FRAG VAUC 7 1 1 3 3 12
NITZ ARCH 1 1 1
DIAT VULG 1 2 1 2 1
CYMB SINU 1
CYMB SILE 2 2 2 1 2 2 2 1
NAVI REIC 2 2 4 2 2 3 1 3 2
NAVI TRIP 4 5 7 2 3 4 2
NAVI SAPR 1 2
NAVI ATOM 3 3
NITZ SOCI 1 1 1
NITZ GFOR 4 1 1
NITZ DISS 4 7 5 3 14 4 8 7 3
NAVI CRTE 2 6 8 3 9 9 14 9 2
NITZ RECT 1 2 1 2 2 1
AMPH LIBY 1 1 2 7 3 5 4 1
NITZ PALE 2 4 2 1 5 6 2 2
NAVI CRCE 1 1 1
ACHN JACK 2 4 5 9
ACHN MINU 2 4 1 10 7 7 14 25
ACHN SAPR 1
NITZ ACIC 1
NITZ GLIS 2 1
RHOI ABBR 3 2 3 6
COCC PEDI 1 1 1 3 22 4 4 8
AMPI PELL 1 2 2 1
NITZ INCT 1
NITZ FRUS 1 1
FRAG PINN 1 1 1 3 1
ACHN LANC 2 1
GOMP SAPR 3
GOMP PARV 1 1 3 1 1 2
STEP HANT 1
NITZ LINE 1
CYMB AMPH 1
NAVI CAPR 1 1 1 1 2 4 7 5 1
CYCL MENE 1 3 5
COCC PLAC 1 1 12 19 3 2 1
NAVI MINI 4 1 1
ACHN DELI 1
NAVI RADI 1 1
FRAG MESO 1
NITZ INCO 1 1
NITZ FONT 1
NITZ LACU 1
GOMP MINU 1 7
CYMB CAES 1
CYMB AFFI 1 4

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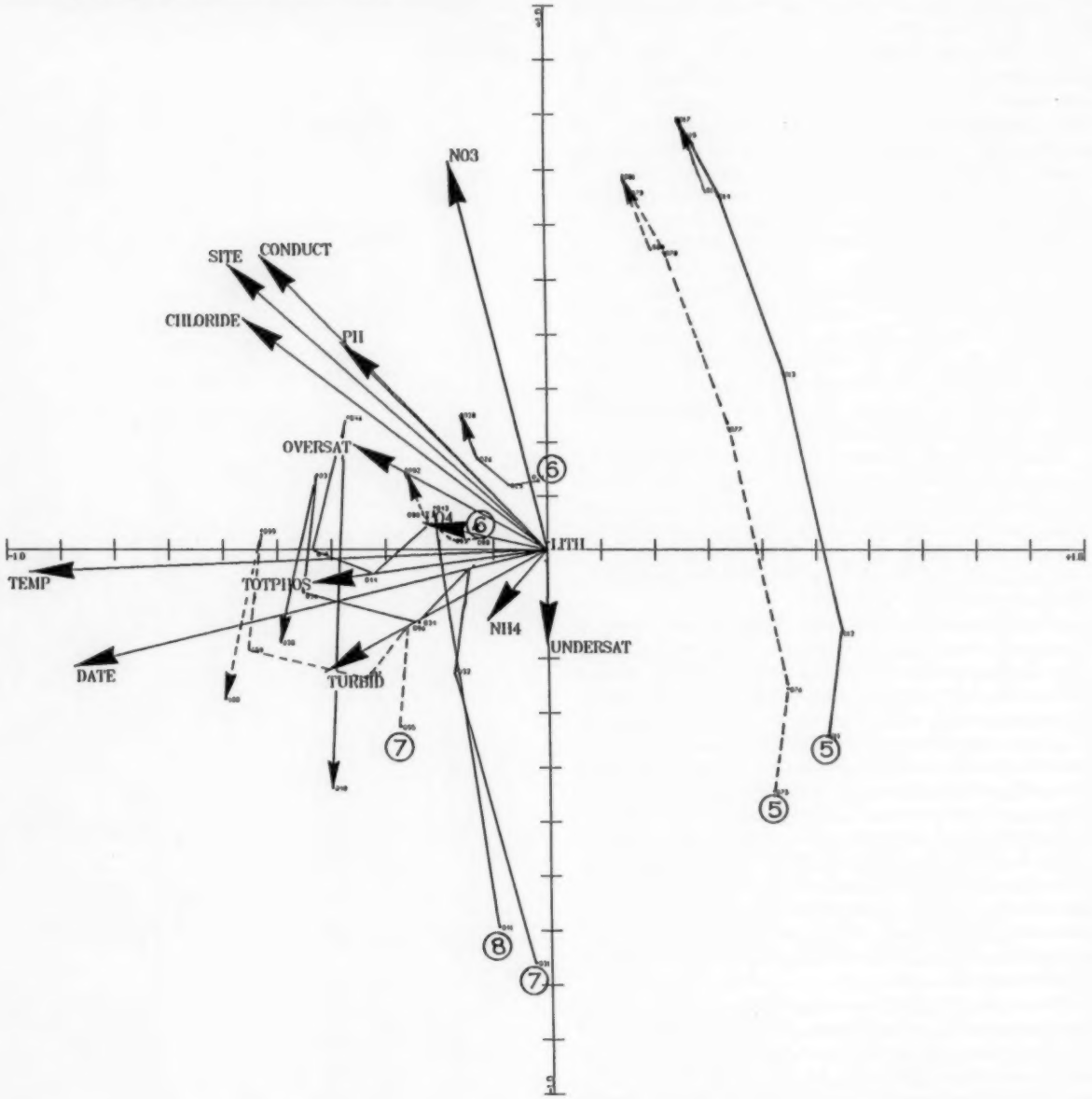
Fig. 4. Ordination of samples according to canonical correspondence analysis relating longitudinal gradients to gradients of environmental variables. Sites are connected by lines, with numbers indicating the uppermost site and arrows pointing towards the lowermost site. Solid lines, stone samples; broken lines, grass; 5–8, May–August.



and therefore most closely related to the site gradient, are conductivity (including noncarbonate conductivity caused by chloride and nutrients) and chloride concentration.

Species-specific preferences (Fig. 5) are strongest for (*i*) summer situations characterized by elevated temperatures, total phosphorus concentrations, and turbidity (*Cyclotella meneghiniana, Cocconeis pediculus, Cocconeis placentula*, and *Amphora libyca*) and for (*ii*) low stream order and discharge (spring samples), low conductivity, and low chloride concentrations irrespective of nutrient levels (*Meridion circulare* and *Fragilaria ulna*). Weaker preferences (species optima less pronounced or correlation for one of the variables not significant) exist for (*iii*) high nitrate values shown by *Surirella brébissonii* and *Navicula lanceolata*, (*iv*) moderate nitrate concentrations (*Navicula gregaria* and *Navicula tripunctata*), (*v*) low stream order and low orthophosphate concentrations (*Gomphonema olivaceum* var. *olivaceum* and *Diatoma tenuis*), and (*vi*) oversaturated midstream sites with

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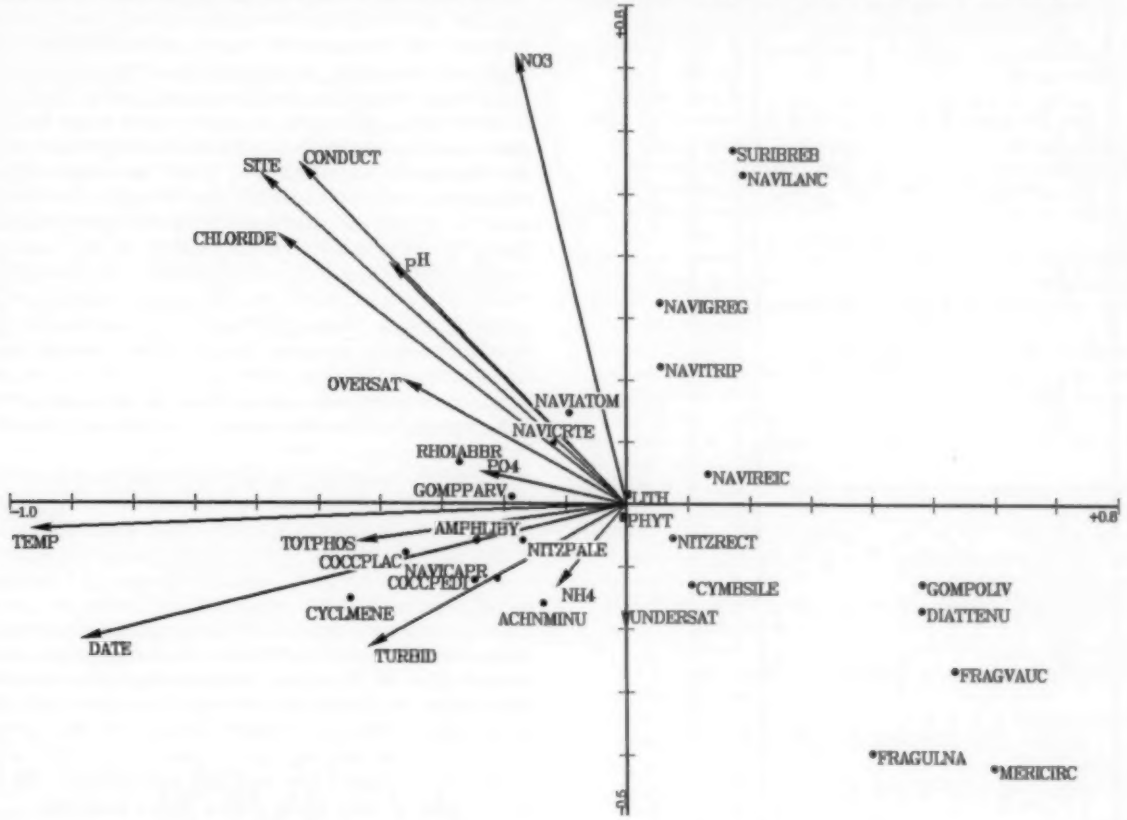
Fig. 5. Correlation of the major environmental variables with diatom species composition and ordination of the 23 species with clearly defined optima for at least one environmental variable determined by canonical correspondence analysis. See Table 2 for species abbreviations.



high orthophosphate (*Rhoicosphenia abbreviata*, *Gomphonema parvulum* var. *parvulum*) and (or) moderate nitrate concentrations (*Navicula atomus* and *Navicula cryptotenella*).

In the data set, most species are arranged along the seasonality vector and in the sector of the low values of nutrients, oversaturation, and stream order (Fig. 5), respectively. The species composition of well-saturated, moderately nutrient-rich situations is best defined. The species set of the polluted areas or even microhabitats affected by likely short-term pulses of nutrients cannot be detected from the present data set. For this purpose, specified microhabitat sampling including biota and water chemical data would be necessary.

The results of the calculation of water quality class and trophic state index (Table 3) show differences by sampling site, season, and substratum. Organic pollution expressed by saprobic water quality class ranges from II (moderate pollution) to III (strong pollution). The trophic status classification ranges between mesotrophic (3.6) and eutrophic (5.3).

Water quality class II could be assigned to all samples at site 2. Sites 1, 3, and 4 were slightly more polluted, and sites 6 and 8 were the most polluted. Indices calculated from epilithic diatoms were lowest for April samples and showed a trend to higher values in July and August. Values from epiphytic diatoms were mostly equal to the values for epilithic diatoms but showed a somewhat higher variability.

Trophic state index at Luther, site 2, showed the lowest values, followed by sites 1, 3, and 10. The more organically polluted midstream and downstream sites are also ranked among the sites with highest nutrient load. Site 4 was only slightly organically polluted, but diatoms indicated high concentrations of inorganic nutrients, compatible with the frequently eutrophic aspect of the site. No seasonal or substratum-dependent trends can be seen from the values in Table 3.

For both indices the statistical evaluation showed that the differences by date and by substratum type are nonsignificant, as are the variations of the results for the majority of the samples from the epilithon. According to Fisher's ANOVA, only site differences were significant and they were more evident for trophic indices ($F = 5.42$, $p < 0.000$) than for saprobic quality classes ($F = 3.54$, $p < 0.001$).

Trophic indices lower than 4.5 always coincide with moderate pollution, while higher trophic indices can be related to each of the saprobic levels found. Thus the combination of both indices distinguishes moderately polluted, eutrophic situations, which are most of the time oxygen saturated and rich in nitrate and orthophosphate, from moderately to strongly or strongly polluted and very eutrophic situations. The latter waters tend to be undersaturated with oxygen and enriched by ammonia and phosphorus.

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Table 3. Saprobic water quality (S)[a] and trophic state (T)[b] for the sampling sites in the Grand River obtained from diatom analysis of epilithic and epiphytic samples.

Site	October 1993		April				May				June				July				August 1994		Total	
	Stone		Stone		Grass		Stone		Grass		Stone		Grass		Stone		Grass		Stone			
	S	T	S	T	S	T	S	T	S	T	S	T	S	T	S	T	S	T	S	T	S	T
1. Keldon	nd	nd	II	4.6	II	4.4	II–III	5.2	III	4.6	II	4.2	II	4.8	II	4.6	II	5.0	II–III	4.6	II (–III)	4.7
2. Luther	nd	nd	II	4.2	II	4.2	II	3.6	II	4.3	II	4.9	II	4.4	II	3.9	II	5.0	II	4.7	II	4.4
3. 10th line	nd	nd	II–III	5.2	II	4.5	II	4.7	II–III	4.8	II	4.7	II	4.8	II–III	4.5	nd	nd	II	4.5	II (–III)	4.7
4. Belwood	II–III	4.8	II–III	5.0	II	4.9	II	5.2	II–III	5.0	II	5.2	II	5.0	II	4.6	II	5.0	II	4.9	II (–III)	5.0
5. Conestogo	nd	nd	II	4.9	II–III	5.0	II	5.0	III	5.0	II–III	4.7	II–III	4.8	II–III	4.8	III	5.1	II	4.7	II–III	4.9
6. Bridgeport	II–III	4.7	II–III	5.0	II–III	4.9	II	5.0	II–III	5.1	III	5.2	III	5.1	III	4.9	II	4.9	III	4.7	II–III (III)	5.0
7. Freeport	II–III	4.8	nd	nd	nd	nd	II–III	5.0	II–III	4.8	II	4.8	II–III	4.6	III	5.2	nd	nd	III	4.8	II–III	4.9
8. Galt	nd	nd	II–III	5.0	II	5.0	III	5.0	II–III	5.0	III	4.6	II–III	4.8	II	5.0	III	5.3	II–III	5.1	II–III (III)	5.0
9. Newport	II–III	4.8	nd	nd	nd	nd	II–III	5.0	II–III	4.9	II	4.7	II–III	4.7	II–III	5.1	III	5.0	II	4.8	II–III	4.9
10. York	nd	nd	II	4.4	II	4.8	II–III	5.0	II–III	5.1	II–III	4.8	III	5.1	II–III	5.2	II	5.0	II–III	4.9	II–III	4.8

[a]Differentiating species groups approach of Lange-Bertalot (from Krammer and Lange-Bertalot 1986): pollution class: II, moderate pollution; II–III, moderate to strong pollution; III, strong pollution; class in parentheses indicates tendency.

[b]Following van Dam et al. (1994): 2, oligotraphentic to mesotraphentic; 3, mesotraphentic; 4, mesotraphentic to eutraphentic; 5, eutraphentic; 6, hypereutraphentic; 7, oligotraphentic to eutraphentic.

Summary and conclusions

The results show clearly that the application of both diatom indicator systems allows for a realistic interpretation of eutrophication and biodegradable organic pollution in the Grand River as evidenced by the chemical data reported here.

Although none of the sites investigated in the Grand River is oligotrophic, differences in trophic status could be monitored using a simple indicator list methodology developed in the Netherlands (van Dam et al. 1994), but using additional information from the literature. The similarity of results obtained from grass and stone samples showed clearly that monitoring of water quality is independent of the choice of substrate, even when silt plays an important role as in the lower reaches of the Grand River. This observation contrasts with the recommendation of Round (1993) who proposed that sampling be restricted to the so-called "true epilithon" obtained after a first washing and brushing of the algal cover. Our results, however, are consistent with a comprehensive study using epilithic and epiphytic samples from streams at different altitudes in Nepal (Rothfritz et al. 1997).

The general ranking of the sites according to diatoms identifies clearly the cleanest and the most affected stations, independent from the season and actual species composition. This applies for the evaluation of both pollution and eutrophication, even when there are some subtle differences in the general classification of the sites. Some differences between the two classifications seem reasonable. An example of this is the average classification of site 4 (Belwood) as moderately polluted but eutrophic. At this station, enhanced organic pollution can be excluded, but a higher nutrient input from the hypolimnion of the upstream reservoir is likely. However, for the two lowermost sites (Newport and York), a decrease of pollution and trophic status is detected by both indicating systems. This can be attributed to progressing mineralization processes of organic substances and to dilution effects along the river course.

The comparison of nutrient concentrations with the 1960s shows clearly that the earlier pattern of pollution and eutrophication remains the same. The lowest water quality remains in the middle reaches; however, progressing eutrophication over the intervening 30 years can be detected mainly by a significant increase in nitrates. This raises the question of what effect nitrate enrichment may have on the river system. As is indicated by the multivariate analysis, in the Grand River, nitrate is not a limiting nutrient for the majority of the periphyton species. However, nitrate enrichment may have a major effect on the oxygen balance of the system by enhancing respiration processes, causing critical low oxygen levels (for fish) during night in the most eutrophicated sections of the river.

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References

Chapman, D. (*Editor*). 1996. Water quality assessment. A guide to the use of biota, sediments and water in environmental monitoring. 2nd ed. E&FN Spon, Chapman and Hall, London, U.K.

Charles, D. 1996. Use of algae for monitoring rivers in the United States: some examples. *In* Use of algae for monitoring rivers II. *Edited by* B.A. Whitton and E. Rott. Institute of Botany, University of Innsbruck, Innsbruck, Austria. pp. 109–118.

Cox, E.J. 1991. What is the basis for using diatoms as monitors of river quality? *In* Use of algae for monitoring rivers. *Edited by* B.A Whitton, E. Rott, and G. Freidrich. Institute of Botany, University of Innsbruck, Innsbruck, Austria. pp. 33–40.

Fraser, S.P.C. 1966. The seasonal growth and distribution of algae in the Grand River. M.Sc.thesis, University of Waterloo, Waterloo, Ont.

GRCA. 1982. Grand River basin water management study. Grand River Implementation Committee, Grand River Conservation Authority, Cambridge, Ont.

Hellebust, J.A., and Lewin, J. 1977. Heterotrophic nutrition. *In* The biology of diatoms. *Edited by* D. Werner. Bot. Monogr. **13**: 169–197.

Hill, M. 1979. TWINSPAN — a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Cornell University, Ithaca, N.Y.

Hofmann, G. 1994. Aufwuchs-Diatomeen in Seen und ihre Eignung als Indikatoren der Trophie. Bibl. Diatomol. **30**.

Kilgour, B.W., Barton, D.R., Dixon, D.G., Duthie, H.C., Fitzgerald, D.G., Goebel, B., Lanno, R.P., Rott, E., and Winter, J.G. 1996. Quantifying stream ecosystem condition: new approaches to developing decision criteria and diagnostic tools. Can. Water Res. J. **21**: 229–235.

Krammer, K., and Lange-Bertalot, H. 1986. Bacillariophyceae 1.Teil: Naviculaceae. *In* Süßwasserflora von Mitteleuropa, Band 2/1. *Edited by* H. Ettl, J. Gerloff, H. Heynig, and D. Mollenhauer. Gustav Fischer Verlag, Stuttgart.

Lange-Bertalot, H. 1979. Pollution tolerance of diatoms as a criterion for water quality estimation. Nova Hedwigia Beih. **64**: 285–305.

Mason, P., Smith, A.F., and Veale, B. 1989. Water quality management in the Grand River basin. Report, Grand River Conservation Authority, Cambridge, Ont.

MOE. 1981. Outline of analytical methods. Ontario Ministry of the Environment, Laboratory Services Branch, Toronto, Ont.

Patrick, R. 1949. A proposed biological measure of stream conditions based on a survey of the Conestoga Basin, Lancaster County, Pennsylvania. Proc. Acad. Nat. Sci. Phila. **101**: 277–341.

Rothfritz, H., Jüttner, I., Suren, A.M., and Ormerod, S.J. 1997. Epiphytic and epilithic communities along environmental gradients in the Nepalese Himalaya: implications for the assessment of biodiversity and water quality. Arch. Hydrobiol. **138**: 465–482.

Rott, E. 1995. Diatoms of the Grand River, Ontario, Canada restudied after 25 years. Limnologica, **25**: 165–192.

Rott, E., Hofmann, G., Pall, K., Pfister, P., and Pipp, E. 1997. Indikationslisten für Aufwuchsalgen in Fließgewässern in Österreich. Teil 1: Saprobielle Indikation. Wasserwirtschaftskataster, Bundesministerium f. Land- und Forstwirtschaft, Wien.

Round, F.E. 1993. A review and methods for the use of epilithic diatoms for detecting and monitoring changes in river water quality. Methods for the examination of waters and associated materials. HMSO, London, U.K.

Sreenivasa, M.R., and Duthie, H.C. 1973. Diatom flora of the Grand River, Ontario, Canada. Hydrobiologia, **42**: 161–224.

Strahler, A.N. 1957. Quantitative analysis of watershed geomorphology. Am. Geophys. Union Trans. **38**: 913–920.

ter Braak, C.J.F. 1988. CANOCO — a FORTRAN program for canonical community ordination by partial detrended canonical correspondence analysis, principal components analysis and redundancy analysis. Agricultural Mathematics Group, Wageningen, The Netherlands.

van Dam, H., Mertens, A., and Sinkeldam, J. 1994. A coded checklist and ecological indicator values of freshwater diatoms from the Netherlands. Neth. J. Aquat. Ecol. **28**: 117–133.

Whitton, B.A., and Kelly, M.G. 1995. Use of algae and other plants for monitoring rivers. Aust. J. Ecol. **20**: 45–56.

Whitton, B.A., and Rott, E. (*Editors*). 1996. Use of algae for monitoring rivers II. Institute of Botany, University of Innsbruck, Innsbruck, Austria.

Winter, J.G., and Duthie, H.C. 1997. Algal monitoring and export coefficient modelling in southern Ontario streams. Sixth Int. Phycol. Congress. Phycologia, **36**: 124. (Abstr.)

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The ontogeny of piscivory and its ecological consequences

Gary G. Mittelbach and Lennart Persson

Abstract: In this study, we review the wealth of ecological information available for 27 species of freshwater piscivores from Europe and North America and examine the factors that determine variation in the diet ontogeny of piscivores and consider some of the ecological consequences of this variation. Focusing on interspecific variation, we found that species that were born larger and had larger mouth gapes became piscivorous at younger ages and at smaller sizes. However, there was no relationship between time of spawning (measured by average spawning temperature) and size at age 1 or size when becoming piscivorous. Species that became piscivorous at smaller sizes were also larger by age 1, and size differences expressed by piscivores in their first year of life tended to carry over to later ages. Not surprisingly, maximum and mean prey size eaten increased with predator size in all species. However, while piscivore species differed in morphologies and feeding efficiencies, prey sizes in the diets were remarkable similar for piscivores of similar body length. These data suggest that most of the variation found in the sizes of prey eaten by piscivores is due to differences in piscivore body size.

Résumé : Dans cette étude, nous passons en revue l'information écologique sur 27 espèces de poissons piscivores d'eau douce d'Europe et d'Amérique du Nord et examinons les facteurs qui déterminent la variation dans l'ontogénie alimentaire des piscivores, et nous considérons certaines des conséquences écologiques de cette variation. En nous concentrant sur la variation interspécifique, nous avons observé que les espèces qui sont de plus grande taille à la naissance et qui ont des ouvertures buccales plus grandes deviennent piscivores à un plus jeune âge et à des tailles plus petites. Toutefois, il n'y avait pas de relation entre le moment de la fraye (établi à partir de la température moyenne au moment de la fraye) et la taille à l'âge de 1 an ou la taille au moment où les poissons deviennent piscivores. Les espèces qui devenaient piscivores à des tailles plus petites étaient aussi plus grosses à l'âge de 1 an, et les différences de taille ainsi observées dans la première année tendaient à se maintenir aux âges plus avancés. Il n'a pas été surprenant d'observer que les tailles maximales et moyennes des proies ingérées s'accroissaient avec la taille des prédateurs chez toutes les espèces. Toutefois, bien qu'on observe chez les espèces piscivores des différences de morphologie et d'efficacité dans l'alimentation, les piscivores de longueurs similaires consommaient des proies de taille remarquablement similaires. Ces données indiquent que la plus grande partie de la variation observée dans les tailles des proies ingérées par les piscivores est attribuable à des différences dans la taille des piscivores. [Traduit par la Rédaction]

Introduction

There is an old saying that "big fish eat little fish." This simple adage illustrates one of the salient features of predator–prey interactions, e.g., predators (generally) are larger than their prey. While this may seem obvious, what is less obvious is how these "big fish" become big. Most fishes begin life as a tiny larva that is far too small to feed on other fish. Therefore, piscivorous species must pass through a series of early life stages where they feed on progressively larger invertebrate prey, eventually becoming large enough to consume other fish. Some species pass through these "ontogenetic niches" (sensu Werner and Gilliam 1984) quickly and begin feeding on fish within a few weeks of birth; other species take years to make the transition. Keast (1985*a*) has termed these two types of predators "specialist piscivores" and "secondary piscivores." Although this dichotomy is a somewhat artificial, it points out important questions, i.e., why do species vary in the timing of the onset of piscivory and what are the ecological consequences of this variation at the individual and population levels?

In this paper, we review the literature for piscivorous fishes from lakes in northern Europe and North America to address these questions. We focus on differences between species. Many traits involved in piscivory also show interesting variation within species. Examining the causes and consequences of this intraspecific variation is an equally important topic, but is beyond the scope of this paper. Here, we have attempted to best characterize average species traits, relying wherever possible on studies that summarize large amounts of data for individual species (e.g., Carlander 1969, 1977; Winemiller and Rose 1992). When studies reported a range of values for a trait within a species, we used the midpoint of the range in our analyses. These comparisons show that pronounced variation exists among species in the onset of piscivory and that this variation is correlated with first-year growth. We examine more closely the factors that potentially drive differences in the ontogeny of piscivory and growth (including piscivore morphology, life history, and growth potential) and consider how these differences among piscivores may affect their diets and impacts on prey communities.

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Table 1. Ontogeny of piscivory within a guild of North American and European piscivorous fishes.

Species	Size when switching to piscivory (mm total length)	Age when first becoming piscivorous (years)	% fish in diet when piscivorous
Piscivorous as YOY			
Bowfin (*Amia calva*)	70–100[ll]	YOY (0+)[ll]	>90[ll]
Burbot (*Lota lota*)	103[kk]	YOY (0+)[aa]	60–99[aa]
Chain pickerel (*Esox niger*)	100–150[c, s]	YOY (0+)[c, s]	>90[kk]
Channel catfish (*Ictalurus punctatus*)	100[f, l]	0+ and 1+[ll]	—
Grass pickerel (*Esox americanus vermiculatus*)	50–150[ll]	0+ and 1+[a]	60–80[a]
Largemouth bass (*Micropterus salmoides*)	50–100[a, b]	0+ and 1+[a, b]	75–95[a, b, ff]
Longnose gar (*Lepisosteus osseus*)	20–50[s, ll]	YOY (0+)[c, s, ll]	>90[s, ll]
Muskellunge (*Esox masquinongy*)	40[s]	YOY (0+)[s]	>90[s]
Northern pike (*Esox lucius*)	45–100[e, i]	YOY (0+)[a, e, i]	>90[ll]
Pikeperch (*Stizostedion lucioperca*)	35–100[f, g, h]	YOY (0+)[f, g, h]	>90[h]
Sauger (*Stizostedion canadense*)	70–110[ee]	YOY (0+)[s, ee]	>90[s, ll]
Sheatfish (*Siluris glanis*)	—	YOY (0+)[y]	—
Smallmouth bass (*Micropterus dolomieu*)	40–100[s, bb]	0+ and 1+[s]	10–40[s, cc]
Walleye (*Stizostedion vitreum*)	35–80[s, k]	YOY (0+)[s, k]	>90[ll]
White bass (*Morone chrysops*)	50–150[dd, gg, ii, jj]	0+ and 1+[ii, jj]	60–100[dd, gg, ii, jj]
Piscivorous after age 1+			
Arctic char (*Salvelinus alpinus*)	130–160[n, v]	2+[n, v]	<10[n, v]
Black crappie (*Pomoxis nigromaculatus*)	140–180[a, ll]	3+ to 4+[a]	25–60[s, ll]
Brook trout (*Salvelinus fontinalis*)	200–300[r]	2+[ll]	5–60[r]
Brown trout (*Salmo trutta*)	130–160[n]	2+[n]	<10[n]
Eurasian perch (*Perca fluviatilis*)	110–160[e, l, m, n]	2+ to 5+[e, l, m, o]	20–90[l, m, p]
Green sunfish (*Lepomis cyanellus*)	50–99[s, ll]	2+ to 3+[w]	10–65[q]
Lake trout (*Salvelinus namaycush*)	150–400[ll]	2+[ll]	>90[ll]
Rock bass (*Ambloplites rupestris*)	100–120[a]	3+ to 4+[a]	20[a]
Warmouth (*Lepomis gulosus*)	125[ll]	3+ to 4+[ll]	6–20[ll]
White perch (*Morone americana*)	110–150[s]	2+[s]	5–70[s, y, z]
Yellow bullhead (*Ameiurus natalis*)	180–240[a]	2+[a]	45[a]
Yellow perch (*Perca flavescens*)	100–170[a, c, d]	4+ to 5+[a, c]	25–60[z]

Note: Species are divided into two groups: those that become piscivorous in their first year of life and those that become piscivorous when older. Source: [a]Keast (1985*a*), [b]Olson (1996), [c]Keast (1977), [d]Johnson (1977), [e]van Densen (1994), [f]Collette and Banarescu (1977), [g]Spanovskaya and Grygorash (1977), [h]Popova and Sytina (1977), [i]Keast and Webb (1966), [j]Mathias and Li (1982), [k]Smith and Pycha (1960), [l]Buijse (1992), [m]Alm (1946), [n]Persson (1983), [o]Persson (1988), [p]Willemsen (1977), [q]Lemly (1985), [r]East and Magnan (1991), [s]Scott and Crossman (1979), [t]Muus and Dahlström (1972), [u]L'Abée-Lund et al. (1992), [v]Johnson and Balon (1980), [w]Hubbs and Cooper (1935), [x]Seaburg and Moyle (1964), [y]Schaeffer and Margraf (1986), [z]Parrish and Margraf (1990), [aa]Bailey (1972), [bb]Carlander (1977), [cc]Probst et al. (1984), [dd]Matthews et al. (1992), [ee]Nelson (1968), [ff]Applegate and Mullan (1967), [gg]Ruelle (1971), [hh]McIlwain (1970), [ii]Priegel (1970), [jj]Ewers and Bosel (1935), [kk]Hanson and Qadri (1980), [ll]Becker (1983).

The piscivore guild

Europe and North America contain a rich collection of lakes formed by the last glaciation. A variety of piscivorous fish occupy these lakes and these species differ in their degree of piscivory. Some species are specialists whose adult diets are >90% fish and some are opportunistic piscivores that only occasionally eat another fish. We examined a group of 27 piscivorous species common to lakes of Europe and eastern North America. In compiling data for this study, we attempted to include as many species as possible from among those native to natural lakes in Europe and eastern North America and for which we could find reasonably complete data on early life history, morphology, growth, and diet. Many of these species are economically important or have an impact on other important fish species, and a great deal of ecological information exists for some of the species. While previous studies have reviewed different aspects of their biology (e.g., Keast and Webb 1966; Marshall 1977; Thorpe 1977; Keast 1985*a*; Craig 1987; Winemiller and Rose 1992), this group of piscivores has never been treated as a whole to look for functional relationships between the development of piscivory and species attributes such as life history, morphology, and growth.

Table 1 lists the species comprising the primary data set. This guild of piscivores includes species from six orders, 10 families, and 15 genera. Three of the species are native to both Europe and North America (burbot (*Lota lota*), northern pike (*Esox lucius*), and Arctic char (*Salvelinus alpinus*)). Two genera, *Stizostedion* and *Perca*, have species represented on both continents (walleye (*Stizostedion vitreum*) and sauger (*Stizostedion canadense*) (North America), pikeperch (*Stizostedion lucioperca*) (Eurasia), yellow perch (*Perca flavescens*) (North

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Table 2. Selected life history characteristics of the piscivore guild.

Species	Egg diameter (mm)	Fecundity (eggs/g)	Hatching length (mm)	Spawning temp. (°C)	Total length age 1 (mm)	Max. total length (mm)	Max. mass (kg wet)	Foraging behavior
Arctic char	3.9–4.3[ee]	—	14–16[gg]	0.5–1.5[ee]	60[ee]	880[o]	10.0[hh]	Group
Black crappie	1.0[j]	60–350[c]	2.5–4.0[x]	18–20[j]	143[aa]	472[aa]	2.5[j]	Group[j, w]
Bowfin	2.2–2.8[w]	10–14[ll]	8.0[ll]	16–19[j]	216[aa]	787[aa]	6.8[j]	Solitary[j]
Brook trout	3.5–5.0[j]	4–7[mm]	20[ll]	Fall	150[aa]	597[aa]	6.6[j]	Solitary[w]
Brown trout	4.9–5.6[hh]	—	19[cc]	6–9[cc]	64[cc, dd]	1000[hh]	15.0[hh]	Solitary
Burbot	1.0–1.5[aa, hh]	49[w, jj]	3[j]	0.5–4.0[hh]	223[aa]	838[aa]	9.0[hh]	—
Chain pickerel	2.0[j]	30[ll]	4.0–7.0[j]	8–11[j]	168[aa]	749[aa]	4.2[j]	Solitary[j]
Channel catfish	3.5–4.0[j]	0.7–12[kk]	6[w]	22–29[j, ll]	147[aa]	976[aa]	26.0[j]	Solitary[w]
Eurasian perch	1.0–2.1[a]	80–201[m, n]	4.1–6.6[a]	5–11[a, g, h]	80[a, m]	500[o]	4.75[o]	Group[s, t]
Grass pickerel	1.5 –2.5[j]	25–35[ll]	5.0–6.0[j, ll]	4–12[j, w]	145[aa]	325[aa]	4.0[j]	Solitary[j]
Green sunfish	1.0–1.4[j]	—	4.6–4.8[j]	20–28[j]	64[aa]	259[aa]	1.0[j]	Solitary[f]
Lake trout	5.0–6.0[j]	0.9–2.6[j]	16[w]	8–11[j]	104[aa]	1240[aa]	46[j]	Solitary[w]
Largemouth bass	1.5–1.7[j]	16–45[c]	5.5–6.5[j]	15–18[j]	117[aa, d]	701[aa]	10.0[j]	Solitary[z]
Longnose gar	2.1–3.2[ll]	7–10[ll]	9–10[w]	17–22[ii, jj]	440[aa]	1370[aa]	23.0[j]	Solitary[j]
Muskellunge	2.5–3.5[j]	12–197[ll]	9.5–10.3[j]	9.5–15[j]	239[aa]	1510[aa]	32.0[j]	Solitary[j, w]
Northern pike	2.5–3.0[j]	25–39[n]	6–8[j]	4–11[j]	116[aa]	1296[aa]	25.0[j]	Solitary[e, s, t, v]
Pikeperch	0.8–1.5[b]	110–260[b]	4.0–5.0[b]	6–12[b]	160[m]	1300[k, o]	18.0[o]	Group (juvenile), solitary (adult)[b, p]
Rock bass	1.7–1.9[w]	7–30[c]	—	16–21[j]	76[aa]	340[aa]	1.5[j]	Solitary[w], group[j]
Sauger	1.0 –1.5[j, aa]	33–88[j]	4.5–6.2[j]	6–11[j]	97[aa]	490[aa]	3.8[j]	Group[j]
Sheatfish	3.0[hh]	7–42[nn]	7.0[hh]	20[hh]	200[hh]	4000[hh]	200.0[hh]	—
Smallmouth bass	1.8–2.2[c]	6–15[j, w]	5.6–5.9[j]	16–18[j]	212[aa]	686[aa]	5.5[j]	Solitary[w]
Walleye	1.4–2.1[b]	30–65[b]	6.0–8.6[b]	6–11[j]	206[aa]	790[aa]	11.0[j]	Group[b, j, u]
Warmouth	0.9–1.0[c, w]	6–33[c]	3.4[w]	21[w]	82[aa]	284[aa]	0.9[w]	Solitary[w]
White bass	0.7–1.2[w]	—	2.0[w]	14–21[j]	115[aa]	381[aa]	2.4[j]	Group[w]
White perch	0.6–0.8[j]	—	2.3[j]	11–15[j]	87[aa]	483[aa]	2.1[j]	Group[oo]
Yellow bullhead	2.0 –3.0[aa, w]	7–10[j]	6[j]	21[j]	64[aa]	330[aa]	1.6[j]	Solitary[w]
Yellow perch	1.0–1.9[a]	190[y]	4.8–6.0[a]	6–14[j]	80[aa]	343[aa]	2.0[j]	Group[j, r]

Note: Source: [a]Thorpe (1977), [b]Marshall (1977), [c]Carlander (1977), [d]Olson (1996), [e]Keast and Webb (1966), [f]Werner and Hall (1977), [g]Spanovskaya and Grygorash (1977), [h]Popova and Sytina (1977), [i]Keast (1977), [j]Johnson (1977), [k]Craig (1987), [l]Scott and Crossman (1979), [m]Willemsen (1977), [n]Craig and Kipling (1983), [o]Maitland (1977), [p]van Densen (1994), [q]Merna et al. (1981), [r]Helfman (1978), [s]Eklöv (1992), [t]Eklöv and Diehl (1994), [u]Ryder (1977), [v]Diana et al. (1977), [w]Becker (1983), [x]Siefert (1969), [y]Brazo et al. (1975), [z]Stroud and Clepper (1975), [aa]Winemiller and Rose (1992), [bb]Muus and Dahlström (1972), [cc]Frost and Brown (1967), [dd]Jensen (1972), [ee]Johnson and Balon (1980), [ff]Bailey (1972), [gg]Balon (1980), [hh]L'Abée-Lund and Hindar (1990), [ii]Dean (1895), [jj]Goff (1984), [kk]Walser and Phelps (1993), [ll]Carlander (1969), [mm]Lachance and Magnan (1990), [nn]Shikhshabekov (1978), [oo]Johnson and Evans (1991).

America), and Eurasian perch (*Perca fluviatilis*) (Eurasia)). The European species are ancestral to the North American species in *Stizostedion* and *Perca* (Collette and Banarescu 1977; Thorpe 1977). The species included in Table 1 represent a wide range of body forms and life histories and encompass much of the variation in piscivore life styles found in north-temperate lakes. We have not attempted to formally control for phylogeny in examining the patterns observed among piscivore life histories, morphologies, growth, and diets. However, when presenting the data, we distinguish among genera and consider the extent to which patterns may be driven by particular taxonomic groups.

The ontogeny of piscivory

In order for a fish to become piscivorous, it must reach a size advantage over its potential prey (usually other young-of-the-year (YOY) fishes). Obtaining a size advantage can occur through a number of routes, including being born earlier, being born at a larger size, or growing faster. We present data for piscivore spawning temperatures (a measure of relative spawning times), egg diameters, and hatching sizes (measures of size at birth) and other ecological factors in Table 2. Trout differ from the other piscivores by spawning in the fall instead of the spring and by having larvae that develop for months within a bed of gravel before emerging. Therefore, we excluded the four trout species when we examined relationships involving the effects of spawning temperature and birth size.

Figure 1 shows that spawning temperature was unrelated to either the size at which a species switched to piscivory or its size at age 1 (Table 3). Thus, while it is generally true that piscivores tend to spawn earlier than their prey (Keast 1985*a*), there is surprisingly no relationship between how early a piscivore spawns and its size at age 1. Size at age 1 and size when shifting to piscivory were, however, correlated with hatching size, and size at age 1 was also correlated with egg diameter (Table 3). In general, the larger the hatching size, the smaller the size when switching to piscivory and the larger the size at age 1. There was also an inverse correlation between the size at which fish become piscivorous and their size after 1 year (Table 3). The above patterns are not strongly driven by any particular taxonomic group, and an examination of the

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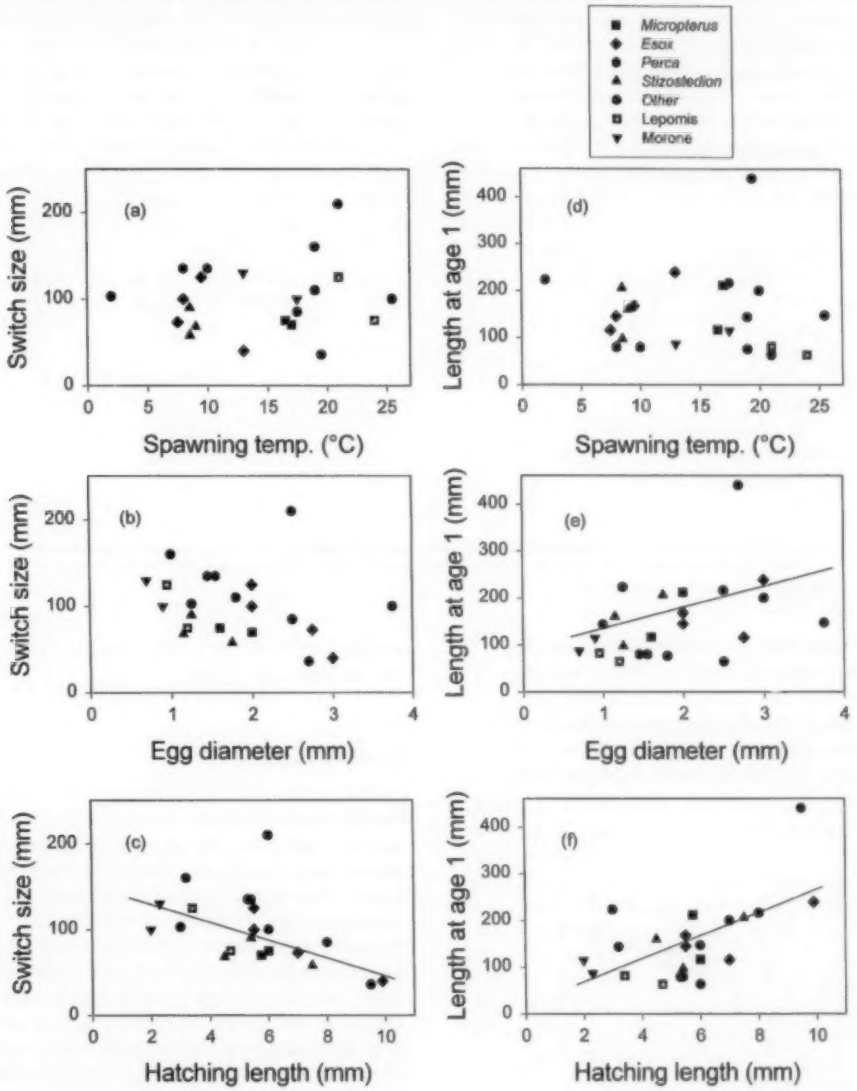
Fig. 1. Relationships between piscivore switch size (i.e., total length when becoming piscivorous) and spawning temperature, egg diameter, and hatching total length and relationships between total length at age 1 (mm) and the above variables. Data are from Tables 1 and 2. Midpoint values were used when a range of values was reported. Species in the same genus are plotted using the same symbol.



distribution of points by genera (Fig. 1) suggests that phylogenetic constraints do not play a major role in affecting the conclusions. However, one relationship that is dependent on phylogeny is the relationship between switch size and maximum size. When all piscivores are included in the analysis, this relationship is weakly negative and not significant (Table 3). However, if trout are excluded, the relationship is strongly negative ($r = -0.64$, $P = 0.001$, $n = 22$), e.g., fish that switch to piscivory at smaller sizes eventually become larger. Trout differ from the other piscivores by reaching a larger maximum size than would be expected based on their switch size.

While hatching size, switch size, and size at age 1 are all correlated, it is not clear how these factors are functionally integrated. Studies with largemouth bass (*Micropterus salmoides*) and other species (e.g., Timmons et al. 1980; Keast and Eadie 1985; Buijse 1992; Olson 1996; van Densen et al. 1996) show that the growth rates of YOY fish may increase dramatically after they switch to feeding on fish. Thus, fish may reach larger sizes at age 1 by switching to piscivory earlier (i.e., at smaller sizes). On the other hand, species may simply differ in their capacity for growth (i.e., maximum potential growth rate), and those species with the highest growth rates may shift to piscivory sooner. To help resolve the latter issue, we examine more closely the growth variation observed among piscivores at each year of their life. We also use

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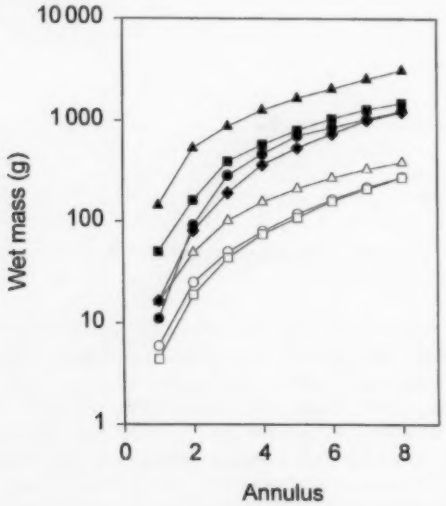
Table 3. Pearson product moment correlations between variables listed in Tables 1 and 2 and illustrated in Fig. 1.

	Spawning temperature	Egg diameter	Hatching length	Switch size	Max. length
Length at age 1					
Correlation coefficient	–0.03	0.42	0.59	–0.46	0.39
P	0.88	<0.05	<0.01	<0.05	<0.05
n	23	23	22	26	27
Spawning temperature					
Correlation coefficient		0.27	0.07	0.12	0.07
P		0.22	0.76	0.59	0.76
n		23	22	22	23
Egg diameter					
Correlation coefficient			0.77	–0.25	0.52
P			<0.0001	0.26	<0.05
n			22	22	23
Hatching length					
Correlation coefficient				–0.52	0.43
P				<0.05	<0.05
n				21	22
Switch size					
Correlation coefficient					–0.22
P					0.28
n					26

Note: Trout are excluded from the analyses involving spawning temperature, egg diameter, and hatching length for reasons stated in the text.

Fig. 2. Average size at age for northern pike (▲), walleye (■), largemouth bass (●), smallmouth bass (◆), black crappie (Δ), yellow perch (○), and rock bass (□) in Michigan lakes. Solid symbols denote species that become piscivorous in their first or second year of life; open symbols denote species that become piscivorous at ages 3+ to 5+. Data are statewide averages from Merna et al. (1981).



experimental data on maximum potential growth rates for the different piscivore species to look at the relationship between potential growth and size at age 1. Finally, we examine whether there are any relationships between fish functional morphology and their switch size and (or) growth patterns during the first year of life.

Growth rates

Realized growth rates

Growth during the first summer appears to be fundamental in determining the size that piscivores reach later in life. For example, there was a positive correlation between size at age 1 and maximum size among all the piscivores studied (Table 3). If we examine size at age for piscivores found in the same geographical region (and therefore experiencing the same climate), we also see that growth during the first year of life is critical in setting the pattern for size at all subsequent ages (Fig. 2). Figure 2 presents average size at age for seven species of piscivores in Michigan lakes (data are statewide averages from Merna et al. 1981). Species that become piscivorous in their first summer (i.e., northern pike and walleye) are substantially larger at age 1 and all subsequent ages than species that switch to piscivory much later in life (i.e., ages 3+ and 4+ for yellow perch, rock bass (*Ambloplites rupestris*) and black crappie (*Pomoxis nigromaculatus*). A similar pattern is found in Europe: piscivores like northern pike and pikeperch reach larger sizes at age 1 than do species like Eurasian perch, brown trout (*Salmo trutta*), and Arctic char (Tables 1 and 2). Largemouth and smallmouth bass (*Micropterus dolomieu*) appear to differ from the other species in Fig. 2 in terms of their general growth trajectory; the bass grow similar to the late-switching species during their first year of life, but then they approach the weights of early-switching piscivores during their second and third years (Fig. 2).

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Fig. 3. Relationships between specific growth rates ($(\ln w_2 - \ln w_1)/(t_2 - t_1)$) at maximum ration at 10°C (■), 15°C (□), 20°C (●), and 25°C (○) and observed size at age 1 (data from Table 2) for (1) northern pike, (2) muskellunge, (3) pikeperch, (4) largemouth bass, (5) Eurasian perch, (6) brown trout, and (7) Arctic char. Data for specific growth rates are from Bevelheimer et al. (1985) (northern pike and muskellunge), Lessmark (1983) (Eurasian perch), Willemsen (1978) (pikeperch), Beamish (1974) and Rice et al. (1983) (largemouth bass), Elliott et al. (1995) (brown trout), and Wandswik and Jobling (1982) and Jobling et al. (1993) (Arctic char, data extrapolated from 14°C).

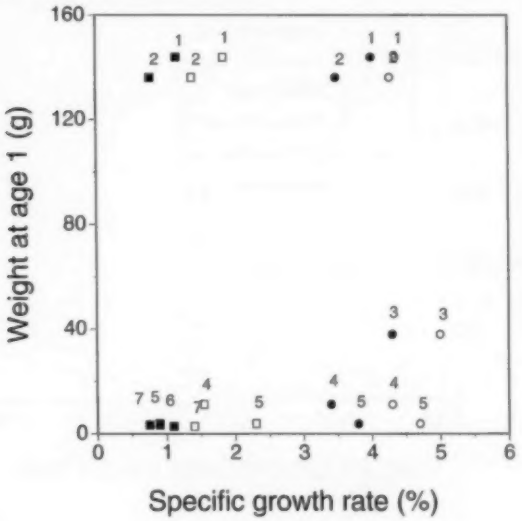
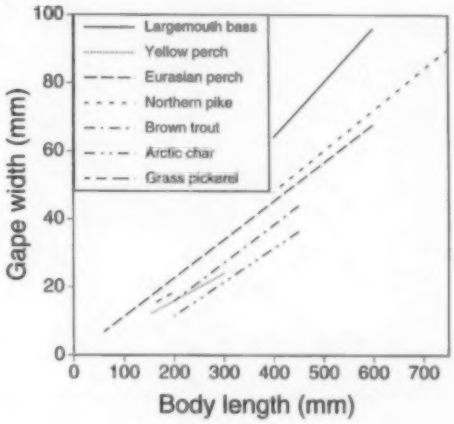


Fig. 4. Gape width – body size relationships for largemouth bass (Keast and Webb 1966), yellow perch (Keast and Webb 1966), Eurasian perch (Christensen 1996), northern pike (Keast and Webb 1966), brown trout (Damsgård 1995), Arctic char (Damsgård 1995), and grass pickerel (*Esox americanus vermiculatus*) (Hoyle and Keast 1988). Data were fitted to a function of the form gape width = $b \times$ body length except for brown trout, Arctic char, and grass pickerel, which had been fitted to the function gape width = $a + b \times$ body length in the original papers. Because of the different functions used to fit the data for brown trout, Arctic char, and grass pickerel in the original papers, the information of significance in the figure is the absolute gape width at a given body length and not the slope.



Growth potential

Are the observed differences in growth among piscivores due to differences in their inherent growth capacities (i.e., different potential growth rates)? We examined this question by evaluating the maximum potential growth rates of the piscivore species at different temperatures. While a number of studies have measured maximum growth rates in the laboratory, these studies often involve limited ranges of fish sizes. Therefore, to make the greatest number of comparisons among species, we calculated maximum growth rates at a fish size of 19.3 g, which was the mean size used by Bevelheimer et al. (1985) for northern pike and muskellunge (*Esox masquinongy*). For pikeperch, maximum growth rate is given for a 14-g fish, which was the size studied by Willemsen (1978).

Regressions of maximum specific growth rate at unlimited ration versus average mass at age 1 (field data) showed that specific growth rate increased with temperature (Fig. 3), which is not surprising. However, no relationship between maximum specific growth rate and mass at age 1 was found at any temperature ($F_{1,4-5} = 0.051–0.39$, $P = 0.58–0.84$), suggesting that differences in growth potentials cannot explain the differences in observed growth trajectories in the field.

Morphology and growth

The above analysis provides little support for the hypothesis that differences in the inherent growth capacities of piscivore species are responsible for generating the observed differences in first-year growth. Instead, it seems more likely that differences in species behaviors, morphologies, and (or) ecological interactions determine how quickly they grow during their first summer of life and that these early growth rates are related to the onset of piscivory. Body morphology is a major factor affecting foraging performance of fish in general, and among piscivores, aspects of body morphology like mouth gape size, fin position, and overall body shape have received considerable attention (Webb 1986; Hoyle and Keast 1987, 1988; Wahl and Stein 1988; Hambright 1991; Christensen 1996). For predators that capture relatively large prey (e.g., piscivores), mouth gape size has been proposed to be a major factor determining the maximum-sized prey a predator can ingest (Hoyle and Keast 1987, 1988).

Gape size – body size relationships have been measured for seven of the piscivore species (Fig. 4) (Ghan and Sprules 1993 also measured gape size – body size relationships for an additional three species at very small body sizes, <50 mm). Largemouth bass have the largest gape width for a specific body length and Arctic char the smallest (Fig. 4). There also exists a clear difference between the perch species, even though the species are closely related. Ideally, one might wish to use a power function to relate gape width (W) to body length (L) (i.e., $W = a \cdot L^b$) for all species to also look for allometric growth within a species and compare allometries among species. However, because most studies report gape width as a direct proportion of body length (i.e., $W = b \cdot L$), or a proportion plus an intercept (i.e., $W = a + b \cdot L$), we were limited to using these relationships in our comparisons. Finally, it should be noted

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Fig. 5. Regressions of size at switch to piscivory (■) and size at age 1 (□) on the slope for the gape width – body size relationships in Fig. 4. Data were ln transformed before entering the analyses. For grass pickerel, brown trout, and Arctic char, where a different regression model had been used (cf. Fig. 4), the slopes were calculated for a 325-mm fish assuming a zero intercept. Compared with Fig. 4, three additional species for which gape width had been measured for small sizes (<50 mm) have been included (i.e., burbot, walleye, and rock bass) (Ghan and Sprules 1993). 1, Largemouth bass; 2, burbot; 3, walleye; 4, northern pike; 5, Eurasian perch; 6, grass pickerel; 7, brown trout; 8, yellow perch; 9, Arctic char; 10, rock bass.

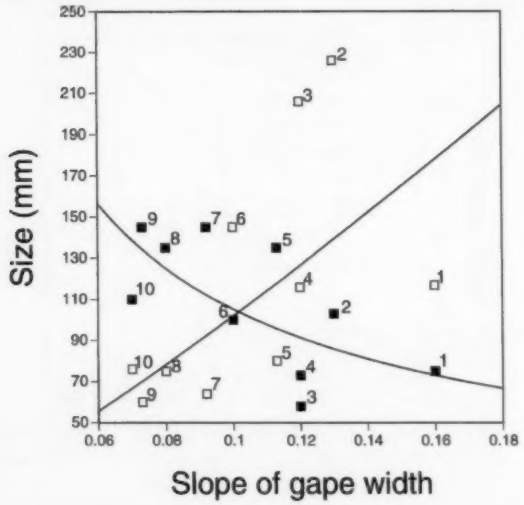
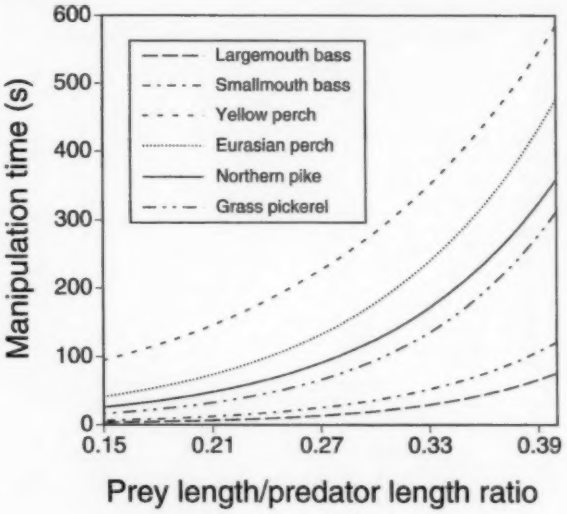


Fig. 6. Prey manipulation time as a function of prey size to predator size ratio for largemouth bass (Hoyle and Keast 1987), smallmouth bass (Winemiller and Taylor 1987), yellow perch (Paszkowski and Tonn 1994), Eurasian perch (Christensen 1996), northern pike (Hart and Hamrin 1988, 1990), and grass pickerel (Hoyle and Keast 1988). Data were fitted to a function of the form prey manipulation time = $1 + a \times \exp(b \times$ prey length/predator length ratio) except for smallmouth bass where data were fitted to a function of the form prey manipulation time = $a \times \exp(b \times$ prey length/predator length ratio).



that while gape width is the most commonly measured metric of predator mouth size, other measures may be equally important in determining the maximum size of prey that can be ingested. For example, in pike, gape depth has been suggested to be a major constraint on maximum prey size taken (Hart and Hamrin 1990).

If we use data from all the species available (i.e., the seven species in Fig. 4 and the three species in Ghan and Sprules 1993), we find that gape width was negatively related to size at switch to piscivory ($F_{1,9} = 5.76$, $P = 0.043$, $r^2 = 0.35$) and positively related to size at age 1 ($F_{1,9} = 6.48$, $P = 0.034$, $r^2 = 0.38$) (Fig. 5). Our interpretation of the pattern for the relationships between gape width, size at switch to piscivory, and size at age 1 is that gape width is a major constraint for the onset of piscivory among YOY piscivores and that this, in turn, affects the size that an individual reaches during its first year of life. Differences in gape width – body size relationships among piscivores also translated into differences in the time required to manipulate prey after capture (Fig. 6), and manipulation time at a predator to prey size ratio of 0.3 was negatively related to gape width ($F_{1,4} = 9.51$, $P = 0.05$). Largemouth bass have the greatest gape widths and the shortest prey manipulations times, while perch have the smallest gape widths and longest manipulation times. Differences among the two perch species in prey manipulation times also agree with their differences in gap size – body size relationships (i.e., Paszkowski and Tonn 1994 versus Christensen 1996). Based on the gape size – body size relationships and the prey manipulation times, we would expect perch to have a lower capacity to handle prey compared with piscivores that shift to piscivory during their first year of life, e.g., northern pike and largemouth bass.

Prey size in diet

The above section documents some of the among piscivore differences in functional morphologies and prey handling capacities and the relationships between these and growth and diet shifts in different piscivore species. Do these differences affect predator diets in the field? For 12 of the species in the piscivore guild, information is available on maximum and mean prey sizes eaten as a function of piscivore length. For a smaller set of species, minimum prey sizes as a function of piscivore size are also available, and these data show that minimum prey size is constant or increases only slowly with piscivore size (Popova and Sytina 1977; Popova 1978; Juanes 1994; van Densen 1994). Earlier interpretations of piscivore diets held that the maximum and mean prey sizes captured by piscivores switching to piscivory at a larger size (e.g., Eurasian perch) were smaller than those of piscivores switching to piscivory at a smaller size (e.g., northern pike and pikeperch). However, based on existing data, it is difficult to discern any pattern between prey size eaten and life history characteristics of the piscivores (e.g., size at switch to piscivory, size at age 1) (Fig. 7).

At larger piscivore sizes, northern pike and brown trout consume the largest fish prey and walleye and muskellunge

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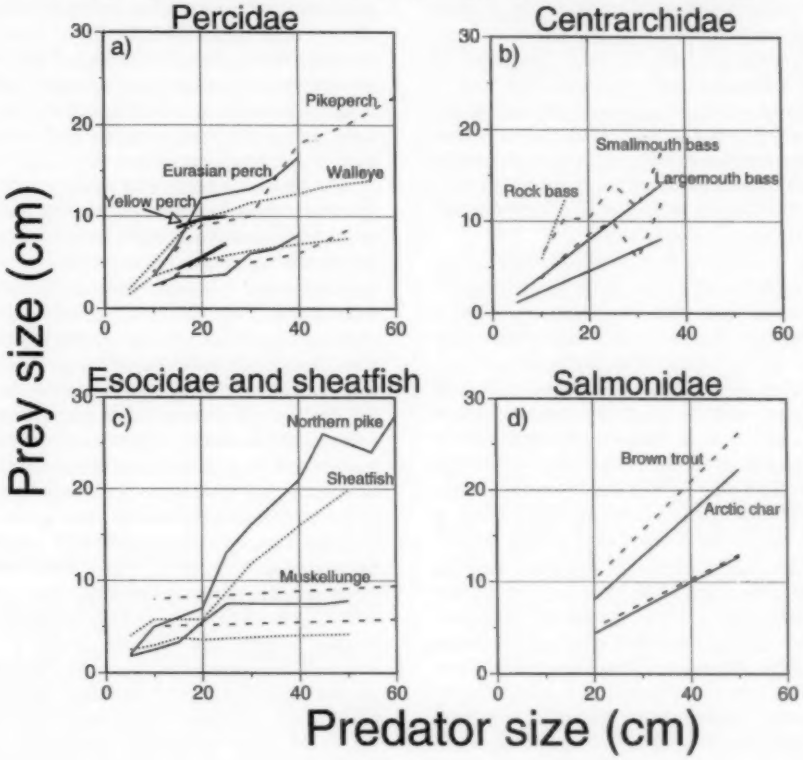
Fig. 7. Maximum and mean prey sizes eaten by Percidae (Eurasian perch, yellow perch, pikeperch, walleye) (Popova and Sytina 1977; Knight et al. 1984; van Densen 1994), Centrarchidae (largemouth bass, smallmouth bass, rock bass) (Probst et al. 1984; Hoyle and Keast 1987; Werner and Hall 1988), Esocidae and sheatfish (northern pike, muskellunge, sheatfish) (Popova and Sytina 1977; Popova 1978; van Densen 1994; Wahl and Stein 1993), and Salmonidae (Arctic char, brown trout) (L'Abée-Lund et al. 1992; Damsgård 1995). Information given is either empirical data (Eurasian perch, pikeperch, northern pike, sheatfish, smallmouth bass, rock bass) or fitted linear equations of prey size versus predator size given in the original papers (brown trout, Arctic char, walleye, largemouth bass, yellow perch).



the smallest fish prey. There was no relationship between the slope of the gape width – body size relationship and either maximum or mean prey sizes eaten by piscivores of 100, 200, or 300 mm ($F_{1,2} = 0.0004–0.243$, $P = 0.66–0.98$, $r^2 = 0.0003–0.075$). Thus, the fact that piscivorous perch on average capture smaller prey than other piscivore species appears not to be due to size-specific differences in feeding capacity, but rather to differences in the average sizes achieved by the different piscivores in nature. Possible explanations for this unexpected lack of a variation in size-specific diet patterns between the species are that the distribution of available prey sizes (most prey fish being small) limits the expression of differences in foraging abilities and (or) that significant differences in prey consumption exist among piscivore species but that they are not measurable by crude variables such as maximum, mean, and minimum prey sizes.

Discussion

There is surprisingly little information on size-specific diets and growth rates of freshwater piscivores during their early life history (but see Keast 1985*b*; Gahn and Sprules 1993). Yet, the available data suggest that factors affecting growth and diet during the first few months of life may be critical to determining piscivore success. For example, Olson et al. (1995) and Olson (1996) examined YOY largemouth bass from a series of natural lakes. Bass in these lakes varied in the size and age at which they became piscivorous, and these differences were due to variation among lakes in the growth rates that bass achieved while feeding on invertebrate prey and in the growth rates of their potential fish prey (i.e., YOY bluegill (*Lepomis macrochirus*)). Basically, in lakes where YOY bass had high growth rates while feeding on invertebrates, they were able to rapidly reach a size advantage over YOY bluegill and shifted to piscivory early. A shift to piscivory was followed by a significant increase in bass growth, and bass sizes at age 1 were largest in lakes where they were consistently able to switch to piscivory during their first summer of life (Olson 1996). Similar patterns have also been found for Eurasian perch and pikeperch (Buijse 1992; Buijse and Houthuijzen 1992). Winemiller and Rose (1992), in a large survey of life history patterns in North American fishes, also found a significant, positive correlation between first-year growth and fish trophic status (trophic classification based on adult diets, i.e., herbivory, omnivory, invertebrativory, and piscivory).

The sparse information available suggests a considerable

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cost in terms of both growth and survival for early-switching species (i.e., those that may become piscivorous during their first year of life), if they do not make the switch (Buijse and Houthuijzen 1992; Olson 1996). Between-year, within-system studies of pikeperch suggest that the onset of piscivory in this species influences both growth and survival, with nonpiscivorous age 0+ pikeperch being in very poor condition (van Densen 1985; Buijse and Houthuijzen 1992; see also Frankiewicz et al. 1996 and van Densen et al. 1996 for the development of bimodality in the size distributions of pikeperch). The onset of piscivory has been shown to affect first-year survival in largemouth and smallmouth bass (e.g., Oliver et al. 1979; Adams et al. 1982; Wicker and Johnson 1987). In contrast, it appears that species that do not normally shift to piscivory during their first year of life may experience effects of piscivory on individual growth but not survival (Buijse 1992).

The cause of these differences in pattern and response are not yet understood. Is there a difference in the developmental biology between piscivore types such that piscivores prone to an early switch to piscivory but that do not shift to piscivory exhibit high mortality due to a rapid decrease in foraging capacity with body size on nonfish prey? In contrast, do piscivores prone to a later shift to piscivory have a slower decrease in foraging capacity with body size on nonfish prey and are they more flexible in their resource use (Eklöv and Persson 1995), thereby buffering against starvation under conditions of low prey fish abundance? Relevant information is lacking, although the studies of Werner (1977) and Persson (1987) suggest that this may be true. We do know that the availability of suitable sizes of prey fish (mainly YOY fish) is important for year-class strength in a number of piscivores switching to piscivory during their first year of life (e.g., Wicker and Johnson 1987; Buijse and Houthuijzen 1992; van Densen et al. 1996).

The above discussion raises a further question: is there a difference in risk taking between piscivores related to their life history? That is, do some piscivores take greater risks to achieve a size that allows them to become piscivorous during their first year of life than do other species, and is this one reason why they grow larger? A number of theoretical studies have examined the potential trade-offs between mortality risk and foraging gain (reviewed in Houston et al. 1993). However, this question is completely unexplored with regard to the ontogeny of piscivory.

We found that differences in mouth morphology among piscivore species were related to two major variables affecting overall growth patterns: size at shift to piscivory and size at age 1. Fish with relatively larger mouth gapes switched to piscivory at smaller sizes and were larger at age 1. Furthermore, differences among piscivores in gape size – body size relationships also translated into differences in prey manipulation times. However, most of the existing estimates of gape size and prey manipulation times are based predominantly on age 1+ and older fish, and we do not know how well these measures apply to younger fish. Quantifying these variables and other measures of functional morphology and feeding performance in age 0+ piscivores is an important area of future research.

One of the more surprising findings of this review was that the sizes of fish eaten by different piscivore species showed relatively little variation when standardized for piscivore length. Two possible explanations for this lack of variation are (*i*) that the distribution of prey sizes available in nature limits the expression of differences in foraging abilities among piscivore species and (*ii*) that significant differences in prey consumption exist among piscivores but that they are not measurable by crude variables such as maximum, mean, and minimum prey sizes. More refined measures of prey capture ability, such as size-specific attack rates, would allow us to compare the feeding efficiencies of different piscivores. With the present knowledge, we can only state that the observed differences in diets between predator species in natural systems appear to be related more to differences in piscivore sizes than to piscivore species per se.

The above sections point to a connection between species-specific morphologies and behaviors and ecological performances of piscivores, as reflected in size at switch to piscivory and size at age 1. Do variations in size at switch to piscivory and size at age 1, in turn, have ramifications for predator–prey relationships? Comparisons of two predator–prey relationships along productivity gradients suggest that this may be true. In a survey of Michigan lakes, Olson et al. (1995) found that largemouth bass biomass increased monotonically with the biomass of its major fish prey (bluegill). However, the relationship between the biomass of Eurasian perch and the biomass on its cyprinid prey is more complex. Depending on environmental conditions (productivity, structural complexity), the relationship between piscivorous perch and prey fish biomass may be either positive or negative (Persson 1988; Persson et al. 1991, 1992). This difference in biomass relationships between these two predator–prey systems is potentially related to the differences in their life history characteristics and feeding morphology (Tables 1 and 2; Figs. 1 and 4–6). Whereas largemouth bass become piscivorous in their first (or second) year of life, it usually takes several years for Eurasian perch to reach the piscivorous stage. This time delay in switching to piscivory may allow competing species to affect the recruitment of perch to the piscivorous stage. Under certain environmental conditions, this leads to a negative relationship between predator and prey biomass across a gradient in lake productivity (Persson 1988). The different relationships between piscivore and prey fish biomass along productivity gradients have also been shown to have feedback effects on other trophic levels (Persson et al. 1992; Mittelbach and Osenberg 1993). It remains to be seen whether the different responses observed in these two predator–prey systems represent general features of systems with early-shifting or late-shifting piscivores or are due to other factors.

In this review, we have tried to synthesize the wealth of data available on the ontogenies, life histories, and feeding relationships of the major freshwater piscivores in northern Europe and eastern North America. In doing so, we have identified a number of gaps in our knowledge of even these well-studied species. For example, it is surprising that such basic data as size-dependent consumption and growth capacity are absent for the majority of species. Also, only a handful of species have been carefully studied with regard to the factors that affect the onset of piscivory within a species (e.g., largemouth bass). For these species, it has been shown that the relative growth rates of YOY piscivores and YOY prey fishes, determined in part by water temperatures and (or) the availability of invertebrate prey, can be crucial in controlling the size at which individuals

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shift to becoming piscivorous (Keast and Eadie 1985; Olson 1996). Size when switching to piscivory was by far the most difficult piece of information to obtain in Tables 1 and 2, and it is also the least-well studied aspect for many species. Ultimately, we would like to be able to assess the relative variation in the onset of piscivory among species and ask whether some species are more variable than others in the onset of piscivory and whether this variation is related to environment, morphology, life history, or other factors. However, this will require better data, particularly studies that compare the onset of piscivory among a number of species from the same lakes (where similar environmental factors are experienced by all species).

In general, studies focused on the first year (or months) in the life history of piscivores should pay large dividends in helping understand the factors that determine predator growth rates, sizes, and abundances. These studies should include both comparative field studies and laboratory studies. Field studies of early diets and associated growth rates are needed, as are laboratory studies of piscivore functional morphologies and feeding abilities at small sizes. In addition, most experimental studies of piscivore foraging capacities have focused on post-capture constraints, specifically handling (manipulation) time. Few studies have covered precapture constraints (e.g., Christensen 1996), which may be of major importance for understanding both food selection in piscivores and observed piscivore – prey fish relationships.

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References

Adams, S.M., McLean, R.B., and Huffman, M.M. 1982. Structuring of a predator population through temperature mediated effects on prey availability. Can. J. Fish. Aquat. Sci. **39**: 1175–1184.

Alm, G. 1946. Reasons for the occurrence of stunted fish populations. Inst. Freshwater Res. Drottningholm Rep. **25**: 1–146.

Applegate, R.L., and Mullan, J.W. 1967. Food of young largemouth bass, *Micropterus salmoides*, in a new and old reservoir. Trans. Am. Fish. Soc. **96**: 74–77.

Bailey, M.M. 1972. Age, growth, reproduction and food of the burbot, *Lota lota* (Linnaeus), in southwestern Lake Superior. Trans. Am. Fish. Soc. **101**: 667–674.

Balon, E.K. 1980. Early ontogeny of the European landlocked Arctic char altricial form *Salvelinus (Salvelinus) alpinus alpinus*. *In* Charrs — salmonid fishes of the genus *Salvelinus*. *Edited by* E.K. Balon. Junk Publishers, The Hague, The Netherlands. pp. 607–630.

Beamish, F.W.H. 1974. Apparent specific dynamic action of largemouth bass, *Micropterus salmoides*. J. Fish. Res. Board Can. **31**: 1763–1769.

Becker, G.C. 1983. Fishes of Wisconsin. University of Wisconsin Press, Madison, Wis.

Bevelheimer, M.S., Stein, R.A., and Carline, R.F. 1985. Assessing significance of physiological differences among three esocids with a bioenergetics model. Can. J. Fish. Aquat. Sci. **42**: 57–69.

Brazo, D.C., Tack, P.I., and Liston, C.R. 1975. Age, growth, and fecundity of yellow perch (*Perca flavescens*) in Lake Michigan near Ludington, Michigan. Trans. Am. Fish. Soc. **104**: 726–230.

Buijse, A.D. 1992. Dynamics and exploitation of unstable percid populations. Ph.D. thesis, Agricultural University, Wageningen, The Netherlands.

Buijse, A.D., and Houthuijzen, R.P. 1992. Piscivory, growth and size-selective mortality of age 0 pikeperch (*Stizostedion lucioperca*). Can. J. Fish. Aquat. Sci. **49**: 894–902.

Carlander, K.D. 1969. Handbook of freshwater fishery biology. Vol. 1. Iowa State University Press, Ames, Iowa.

Carlander, K.D. 1977. Handbook of freshwater fishery biology. Vol. 2. Iowa State University Press, Ames, Iowa.

Christensen, B. 1996. Predator foraging capabilities and prey antipredator behaviours: pre- versus post-capture constraints on size-dependent predator-prey interactions. Oikos, **76**: 368–380.

Collette, B.B., and Banarescu, P. 1977. Systematics and zoogeography of the fishes of the family Percidae. J. Fish. Res. Board Can. **34**: 1450–1463.

Craig, J.F. 1987. The biology of the perch and related fish. Croom Helm, London, U.K.

Craig, J.F., and Kipling, C. 1983. Reproduction effort versus the environment: case histories of Windermere perch, *Perca fluviatilis* L., and pike, *Esox lucius* L. J. Fish Biol. **22**: 713–727.

Damsgård, B. 1995. Arctic charr, *Salvelinus alpinus* (L.), as prey for piscivorous fish — a model to predict prey vulnerabilities and prey size refuges. Nord. J. Freshwater Res. **71**: 190–196.

Dean, B. 1895. The early development of garpike and sturgeon. J. Morphol. **11**: 1–62.

Diana, J.S., MacKay, W.C., and Ehrman, M. 1977. Movements and habitat preference of northern pike (*Esox lucius*) in Lac Ste. Anne, Alberta. Trans. Am. Fish. Soc. **106**: 560–565.

East, P., and Magnan, P. 1991. Some factors regulating piscivory of brook trout, *Salvelinus fontinalis*, in lakes of the Laurentian Shield. Can. J. Fish. Aquat. Sci. **48**: 1735–1743.

Eklöv, P. 1992. Group foraging versus solitary foraging efficiency in piscivorous predators: the perch, *Perca fluviatilis*, and pike, *Esox lucius*, patterns. Anim. Behav. **44**: 313–326.

Eklöv, P., and Diehl, S. 1994. Piscivore efficiency and refuging prey: the importance of predator search mode. Oecologia, **98**: 344–353.

Eklöv, P., and Persson, L. 1995. Species-specific antipredator capacities and prey refuges: Interactions between piscivorous perch (*Perca fluviatilis*) and juvenile perch and roach (*Rutilus rutilus*). Behav. Ecol. Sociobiol. **37**: 169–178.

Elliott, J.M., Hurley, M.A., and Fryer, R.J. 1995. A new, improved growth model for brown trout, *Salmo trutta*. Funct. Ecol. **9**: 290–298.

Ewers, L.A., and Bosel, M.W. 1935. The food of some Buckeye Lakes fishes. Trans. Am. Fish. Soc. **65**: 57–68.

Frankiewicz, P., Dabrowski, K., and Zalewski, M. 1996. Mechanism of establishing bimodality in a size distribution of age-0 pikeperch, *Stizostedion lucioperca* (L.) in the Sulejów reservoir, central Poland. Ann. Zool. Fenn. **33**: 321–327.

Frost, W.E., and Brown, M.E. 1967. The trout. NMN Collins, London, U.K.

Ghan, D., and Sprules, W.G. 1993. Diet, prey selection, and growth of larval and juvenile burbot *Lota lota* (L.). J. Fish Biol. **42**: 47–64.

Goff, G.P. 1984. The brood care of longnose gar (*Lepisosteus osseus*) by smallmouth bass (*Micropterus dolomieui*). Copeia, 1984: 149–152.

Hambright, K.D. 1991. Experimental analysis of prey selection by largemouth bass: role of predator mouth width and prey body depth. Trans. Am. Fish. Soc. **120**: 501–508.

Hanson, J.M., and Qadri, S.V. 1980. Morphology and diet of young-of-year bubot, *Lota lota*, in the Ottawa river. Can. Field-Nat. **94**: 311–314.

© 1998 NRC Canada

Hart, P.J.B., and Hamrin, S.F. 1988. Pike as a selective predator. Effects of prey size, availability, cover and pike jaw dimensions. Oikos, **51**: 220–226.

Hart, P.J.B., and Hamrin, S.F. 1990. The role of behaviour and morphology in the selection of prey by pike. *In* behavioural mechanisms of food selection. *Edited by* R.N. Hughes. NATO ADI Ser. G 20. Springer-Verlag, Berlin. pp. 235–254.

Helfman, G.S. 1978. Patterns of community structure in fishes: summary and overview. Environ. Biol. Fishes, **3**: 129–148.

Houston, A.I., McNamara, J.M., and Hutchinson, J.M.C. 1993. General results concerning the trade-off between gaining energy and avoiding predation. Philos. Trans. R. Soc. Lond. B Biol. Sci. **341**: 375–397.

Hoyle, J.A., and Keast, A. 1987. The effects of prey morphology and size on handling time in a piscivore, the largemouth bass (*Micropterus salmoides*). Can. J. Zool. **65**: 1972–1977.

Hoyle, J.A., and Keast, A. 1988. Prey handling time in two piscivores, (*Esox americanus vermiculatus*) and (*Micropterus salmoides*), with contrasting mouth morphologies. Can. J. Zool. **66**: 540–542.

Hubbs, C.L., and Cooper, G.P. 1935. Age and growth of the longeared and the green sunfishes in Michigan. Pap. Mich. Acad. Sci. Arts Lett. **20**: 669–696.

Jensen, K.W. 1972. On the dynamics of an exploited population of brown trout (*Salmo trutta* L.). Inst. Freshwater Res. Drottingholm Rep. **52**: 34–40.

Jobling, M., Jørgensen, E.H., Arnesen, A.M., and Ringø, E. 1993. Feeding, growth and environmental requirements of Arctic charr, a review of aquaculture potential. Aquacult. Int. **1**: 20–46.

Johnson, F.H. 1977. Responses of walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*) populations to the removal of white sucker (*Catostomus commersoni*) from a Minnesota lake, 1966. J. Fish. Res. Board Can. **34**: 1633–1642.

Johnson, L., and Balon, E.K. 1980. The Arctic charr. *In* Charrs — salmonid fishes of the genus *Salvelinus*. *Edited by* E.K. Balon. Junk Publishers, The Hague, The Netherlands. pp. 607–630.

Johnson, T.B., and Evans, D.O. 1991. Behaviour, energetics, and associated mortality of young-of-year white perch (*Morone americana*) and yellow perch (*Perca flavescens*) under simulated winter conditions. Can. J. Fish. Aquat. Sci. **48**: 672–680.

Juanes, F. 1994. What determines prey size selectivity in piscivorous fishes? *In* Theory and application in fish feeding ecology. *Edited by* D.J. Stouder, K.L. Fresh, and R.J. Feller. University of South Carolina Press, Columbia, S.C. pp. 79–100.

Keast, A. 1977. Diet overlap and feeding relationships between the year classes in the yellow perch (*Perca flavescens*). Environ. Biol. Fishes, **2**: 53–70.

Keast, A. 1985*a*. The piscivore feeding guild of the fishes in small freshwater ecosystems. Environ. Biol. Fishes, **12**: 119–129.

Keast, A. 1985*b*. Development of dietary specialization in a summer community of juvenile fishes. Environ. Biol. Fishes, **13**: 211–224.

Keast, A., and Eadie, J.M. 1985. Growth depensation in year-0 largemouth bass: the influence of diet. Trans. Am. Fish. Soc. **114**: 204–213.

Keast, A., and Webb, D. 1966. Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. J. Fish. Res. Board Can. **23**: 1845–1874.

Knight, R.L., Margraf, F.J., and Carline, R.G. 1984. Piscivory by walleyes and yellow perch in western Lake Erie. Trans. Am. Fish. Soc. **113**: 677–693.

L'Abée-Lund, J.H., and Hindar, K. 1990. Interpopulation variation in reproductive traits of anadromous female brown trout, *Salmo trutta* L. J. Fish Biol. **37**: 755–763.

L'Abée-Lund, J.H., Langeland, A., and Saegrov, H. 1992. Piscivory by brown trout (*Salmo trutta* L.) and Arctic charr (*Salvelinus alpinus* L.) in Norwegian lakes. J. Fish Biol. **41**: 91–101.

Lachance, S., and Magnan, P. 1990. Comparative ecology and behavior of domestic, hybrid, and wild strains of brook trout, *Salvelinus fontinalis*, after stocking. Can. J. Fish. Aquat. Sci. **47**: 2285–2292.

Lemly, A.D. 1985. Suppression of native fish populations by green sunfish in first-order streams of Piedmont North Carolina. Trans. Am. Fish. Soc. **114**: 705–712.

Lessmark, O. 1983. Competition between perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) in south Swedish lakes. Ph.D. thesis, University of Lund, Lund, Sweden.

Maitland, P.S. 1977. The Hamlyn guide to freshwater fishes of Britain & Europe. Hamlyn, London.

Marshall, T.R. 1977. Morphological, physiological, and ethological differences between walleye (*Stizostedion vitreum vitreum*) and pikeperch (*S. lucioperca*). J. Fish. Res. Board Can. **34**: 1515–1523.

Mathias, J.A., and Li, S. 1982. Feeding habits of walleye larvae and juveniles: comparative laboratory and field studies. Trans. Am. Fish. Soc. **111**: 722–735.

Matthews, W.J., Gelwick, F.P., and Hoover, J.J. 1992. Food and habitat use by juveniles of species of *Micropterus* and *Morone* in a southwestern reservoir. Trans. Am. Fish. Soc. **121**: 54–66.

McIlwain, T.D. 1970. Stomach contents and length–weight relationships of chain pickerel (*Esox niger*) in southern Mississippi waters. Trans. Am. Fish. Soc. **99**: 439–440.

Merna, J.W., Schneider, J.C., Alexander, G.R., Alward, W.D., and Eshenroder, R.L. 1981. Manual of fisheries survey methods. Fish. Manage. Rep. No. 9, Michigan Department of Natural Resources, Ann Arbor, Mich.

Mittelbach, G.G., and Osenberg, C.W. 1993. Stage-structured interactions in bluegill: consequences of adult resource variation. Ecology, **74**: 2381–2394.

Muus, G.J., and Dahlström, P. 1972. Sötvattensfisk och Fiske. Nordstedt, Stockholm, Sweden. (In Swedish.)

Nelson, W.R. 1968. Reproduction and early life history of sauger, *Stizostedon canadense*, in Lewis and Clark Lake. Trans. Am. Fish. Soc. **97**: 159–166.

Oliver, T.D., Holeton, G.F., and Chua, K.E. 1979. Overwinter mortality of fingerling smallmouth bass in relation to size, relative energy stores, and environmental temperatures. Trans. Am. Fish. Soc. **108**: 130–136.

Olson, M.H. 1996. Ontogenetic niche shifts in largemouth bass: variability and consequences for first-year growth. Ecology, **77**: 179–190.

Olson, M.H., Mittelbach, G.G., and Osenberg, C.W. 1995. Competition between predator and prey: resource-based mechanisms and implications for stage-structured dynamics. Ecology, **76**: 1758–1771.

Parrish, D.L., and Margraf, F.J. 1990. Interactions between white perch (*Morone americana*) and yellow perch (*Perca flavescens*) in Lake Erie as determined by feeding and growth. Can. J. Fish. Aquat. Sci. **47**: 1779–1787.

Paszkowski, C.A., and Tonn, W.M. 1994. Effects of prey size, abundance, and population structure on piscivory by yellow perch. Trans. Am. Fish. Soc. **123**: 855–865.

Persson, L. 1983. Food consumption and competition between age classes in a perch (*Perca fluviatilis*) population in a shallow eutrophic lake. Oikos, **40**: 197–207.

Persson, L. 1987. Effects of resource availability and distribution on size class competition in perch (*Perca fluviatilis*). Oikos, **48**: 148–160.

Persson, L. 1988. Asymmetries in competitive and predatory interactions in fish populations. *In* Size-structured populations — ecology and evolution. *Edited by* B. Ebenman and L. Persson. Springer-Verlag, Berlin. pp. 203–218.

Persson, L., Diehl, S., Jonansson, L., Anderson, G., and Hamrin, S. 1991. Shifts in fish communities along the productivity gradient of temperate lakes — patterns and the importance of size-structured interactions. J. Fish Biol. **38**: 281–293.

Persson, L., Diehl, S., Jonansson, L., Anderson, G., and Hamrin, S. 1992. Trophic interactions in temperate lake ecosystems: a test of food chain theory. Am. Nat. **140**: 59–84.

© 1998 NRC Canada

Popova, O.A. 1978. The role of predaceous fish in ecosystems. *In* Ecology of freshwater fish production. *Edited by* S.D. Gerking. Blackwell Scientific Publications, Oxford, U.K. pp. 215–249.

Popova, O.A., and Sytina, L.A. 1977. Food and feeding relations of Eurasian perch (*Perca fluviatilis*) and pikeperch (*Stizostedion lucioperca*) in various waters of the USSR. J. Fish. Res. Board Can. **34**: 1559–1570.

Priegel, G.R. 1970. Food of white bass, *Roccus chrysops*, in Lake Winnebago, Wisconsin. Trans. Am. Fish. Soc. **99**: 440–443.

Probst, W.E., Rabeni, C.F., Covington, W.G., and Marteney, R.E. 1984. Resource use by stream-dwelling rock bass and smallmouth bass. Trans. Am. Fish. Soc. **113**: 283–294.

Rice, J.A., Breck, J.E. Bartell, S.M., and Kitchell, J.F. 1983. Evaluating the constraints of temperature, activity and consumption on growth of largemouth bass. Environ. Biol. Fishes, **9**: 263–275.

Ruelle, R. 1971. Factors influencing growth of white bass in Lewis and Clark Lake. *In* Reservior fisheries and limnology. *Edited by* G.E. Hall. Am. Fish. Soc. Spec. Publ. No. 8.

Ryder, R.A. 1977. Effects of ambient light variations on behavior of yearling, subadult, and adult walleyes (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. **34**: 1481–1491.

Schaeffer, J.S., and Margraf, F.J. 1986. Food of white perch (*Morone americana*) and potential competition with yellow perch (*Perca flavescens*) in Lake Erie. Ohio J. Sci. **86**: 26–29.

Scott, W.B., and Crossman, E.J. 1979. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. No. 184.

Seaburg, K.C., and Moyle, J.B. 1964. Feeding habits, digestion rates, and growth of some Minnesota warm water fishes. Trans. Am. Fish. Soc. **93**: 269–285.

Shikhshabekov, M.M. 1978. The sexual cycles of the catfish, *Silurs glanis*, the pike, *Esox lucius*, the perch, *Perca fluviatilis*, and the pike-perch, *Stizostedion lucioperca*. J. Ichthyol. **18**: 457–468.

Siefert, R.E. 1969. Characteristics for separation of white and black crappie larvae. Trans. Am. Fish. Soc. **98**: 326–328.

Smith, L.L., Jr., and Pycha, R.L. 1960. First-year growth of the walleye, *Stizostedion vitreum vitreum* (Mitchell), and associated factors in the Red Lakes, Minnesota. Limnol. Oceanogr. **5**: 281–290.

Spanovskaya, V.D., and Grygorash, V.A. 1977. Development and food of age 0 Eurasian perch (*Perca fluviatilis*) in reservoirs near Moscow, USSR. J. Fish. Res. Board Can. **34**: 1551–1558.

Stroud, R.H., and Clepper, H. 1975. Black bass biology and management. Sport Fishing Institute, Washington, D.C.

Thorpe, J.E. 1977. Morphology, physiology, behavior, and ecology of *Perca fluviatilis* L. and *Perca flavescens* Mitchill. J. Fish. Res. Board Can. **34**: 1504–1514.

Timmons, T.J., Shelton, W.L., and Davies, W.D. 1980. Differential growth of largemouth bass in West Point Reservoir, Alabama–Georgia. Trans. Am. Fish. Soc. **109**: 176–186.

van Densen, W.L.T. 1985. Piscivory and the development of bimodality in the size distribution of 0+ pikeperch (*Stizostedion lucioperca* L.). J. Appl. Ichthyol. **1**: 119–131.

van Densen, W.L.T. 1994. Predator enhancement in freshwater fish communities. *In* Rehabilitation of freshwater fisheries. *Edited by* I.G. Cowx. Fishing News Books, Blackwell Scientific Publications, Oxford, U.K. pp. 102–119.

van Densen, W.L.T., Ligtvoet, W., and Roozen, R.W.M. 1996. Intracohort variation in the individual size of juvenile pikeperch, *Stizostedion lucioperca*, and perch, *Perca fluviatilis*, in relation to the size spectrum of their food items. Ann. Zool. Fenn. **33**: 495–506.

Wahl, D.H., and Stein, R.A. 1988. Selective predation by three esocids: the role of prey behavior and morphology. Trans. Am. Fish. Soc. **117**: 142–151.

Wahl, D.H., and Stein, R.A. 1993. Comparative population characteristics of muskellunge, northern pike, and their hybrid. Can. J. Fish. Aquat. Sci. **50**: 1961–1968.

Walser, C.A., and Phelps, R.P. 1993. Factors influencing the enumeration of channel catfish eggs. Prog. Fish-Cult. **55**: 195–198.

Wandswik, A., and Jobling, M. 1982. Observations on growth rates of Arctic charr, *Salvelinus alpinus* (L.), reared at low temperatures. J. Fish Biol. **20**: 689–699.

Webb, P.W. 1986. Locomotion and predator–prey relationships. *In* Predator–prey relationships: perspectives and approaches from the study of lower vertebrates. *Edited by* M.E. Feder and G.V. Lauder. University of Chicago Press, Chicago, Ill. pp. 24–41.

Werner, E.E. 1977. Species packing and niche complementarity in three sunfishes. Am. Nat. **11**: 553–578.

Werner, E.E., and Gilliam, J.F. 1984. The ontogenetic niche and species interactions in size-structured populations. Annu. Rev. Ecol. Syst. **15**: 393–426.

Werner, E.E., and Hall, D.J. 1977. Competition and habitat shift in two sunfishes (Centrarchidae). Ecology, **58**: 869–876.

Werner, E.E., and Hall, D.J. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate – predation risk tradeoff. Ecology, **69**: 1352–1366.

Wicker, A.M., and Johnson, W.E. 1987. Relationships among fat content, condition factor, and first-year survival of Florida largemouth bass. Trans. Am. Fish. Soc. **116**: 264–271.

Willemsen, J. 1977. Population dynamics of percids in Lake Issel and some smaller lakes in the Netherlands. J. Fish. Res. Board Can. **34**: 1710–1718.

Willemsen, J. 1978. Influence of temperature on feeding, growth and mortality of pikeperch and perch. Verh. Int. Ver. Limnol. **20**: 2127–2133.

Winemiller, K.O., and Rose, K.A. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. Can. J. Fish. Aquat. Sci. **49**: 2196–2218.

Winemiller, K.O., and Taylor, D.H. 1987. Predatory behaviour and competition among laboratory-housed largemouth and smallmouth bass. Am. Midl. Nat. **117**: 148–166.

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Multiyear tagging studies incorporating fishing effort data

John M. Hoenig, Nicholas J. Barrowman, William S. Hearn, and Kenneth H. Pollock

Abstract: The Brownie models for multiyear tagging studies can be used to estimate age- and year-specific annual survival rates and tag recovery rates. The latter are composites of the exploitation rates and rates of tag reporting, tag shedding, and tag-induced mortality. It is possible to estimate the exploitation rates if the other components of the tag recovery rates can be quantified. Instantaneous rates of fishing and natural mortality can be estimated if information is available on the seasonal distribution of fishing effort. The estimated rates are only moderately dependent on the timing of the fishing; consequently, the relative effort data can be crude. Information on the timing of the catch over the course of the year can be used as a substitute for the effort data. Fishing mortality can also be assumed to be proportional to fishing effort over years; consequently, if fishing effort is known then the tag reporting rate, natural mortality rate, and a single catchability coefficient can be estimated (instead of natural mortality and a series of fishing mortalities). Although it is possible in theory to estimate both the tag reporting rate and the natural mortality rate with all of these models, in practice it appears necessary to obtain some additional data relating to tag reporting rate to obtain acceptable results. The additional data can come from a variable reward tagging study, a creel or port sampling survey, or from tagged animals that are secretly added to the fishers' catches.

Résumé : Les modèles de Brownie utilisés pour des études de marquage pluriannuelles peuvent servir à évaluer le taux de survie et le taux de récupération des marques pour des âges et des années donnés. Le taux de récupération des marques est un composite du taux d'exploitation et des taux de déclaration des marques, de pertes des marques et de la mortalité induite par les marques. On peut estimer les taux d'exploitation si les autres composantes du taux de récupération des marques peuvent être mesurées. Les taux instantanés de mortalité par pêche et de mortalité naturelle peuvent être évalués si on possède des données sur la répartition saisonnière de l'effort de pêche. Les taux estimés n'étant que modérément dépendants de la période de pêche, les données relatives sur l'effort peuvent donc être grossières. On peut remplacer les données sur l'effort par les données sur la période de capture au cours de l'année. On peut aussi supposer que la mortalité par pêche est proportionnelle à l'effort de pêche au cours des années; donc, si l'effort de pêche est connu, on peut alors évaluer le taux de déclaration des marques, le taux de mortalité naturelle et un coefficient unique de capturabilité (plutôt que la mortalité naturelle et une série de taux de mortalité par pêche). Tous ces modèles permettent d'évaluer théoriquement le taux de déclaration des marques et le taux de mortalité naturelle; mais, dans la pratique, il faudrait d'autres données sur le taux de déclaration des marques afin d'obtenir des résultats acceptables. Ces autres données peuvent provenir d'une étude de marquage avec récompense variable, d'une enquête sur la pêche sportive ou d'un échantillonnage au port, ou d'animaux marqués qui sont ajoutés à l'insu de pêcheurs dans leurs prises.
[Traduit par la Rédaction]

Introduction

Brownie et al. (1978, 1985) developed a series of models for multiyear tagging studies that allow one to estimate age- and year-specific survival rates and tag recovery rates. The latter are composite parameters involving tag retention, exploitation, tag-induced mortality, and tag reporting rates and, therefore, are uninteresting parameters by themselves. The Brownie models generalize early work by Seber (1970) and Robson and Youngs (1971). Although Youngs and Robson (1975) applied their model to a study of lake trout (*Salvelinus namaycush*), it has only been recently that this class of models and its extensions have received much attention in fisheries research (Jagielo 1991; Larson et al. 1991; Pollock et al. 1991; Dorazio 1992; Schwarz et al. 1993).

Pollock et al. (1991) showed that, when additional information on the retention–survival rate and tag reporting rate is available, one can estimate the exploitation rate from the recovery rate parameter. If additional information is available on the seasonal distribution of fishing intensity, then it is possible to determine the instantaneous rates of fishing and natural mortality. Pollock et al. (1991, 1994) considered two special cases: constant fishing effort over the year and effort confined to a short pulse.

The Brownie models are extremely useful. However, a valid criticism is that they may not make use of all available information. For example, they do not take the magnitude of the fishing effort into consideration, and they do not include a

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Table 1. Expected and observed number of tag recoveries in a multiyear tagging study (model 1).

Year	No. tagged	Year 1	2	3	4
Expected recoveries					
1	N_1	$N_1 f_1$	$N_1 S_1 f_2$	$N_1 S_1 S_2 f_3$	$N_1 S_1 S_2 S_3 f_4$
2	N_2	—	$N_2 f_2$	$N_2 S_2 f_3$	$N_2 S_2 S_3 f_4$
3	N_3	—	—	$N_3 f_3$	$N_3 S_3 f_4$
Observed recoveries					
1	N_1	r_{11}	r_{12}	r_{13}	r_{14}
2	N_2	—	r_{22}	r_{23}	r_{24}
3	N_3	—	—	r_{33}	r_{34}

Note: Symbols are as follows: S_j, survival rate in year j; f_j, tag recovery rate in year j; r_{ij}, number of tags recovered in year j from animals tagged in year i.

functional relationship between survival rate and tag recovery rate. A second criticism is that the models are parameterized in terms of finite mortality rates instead of the instantaneous rates generally used by fisheries biologists. It would be valuable to be able to estimate the natural mortality rate. Furthermore, one might wish to impose restrictions on the component mortality rates, e.g., to specify constant natural mortality.

In this paper we concentrate on ways in which information on fishing effort may be used in the analysis of tagging data. We develop two approaches, one of which has a weak dependence on the effort data while the other has a strong dependence. For the former, the pattern of effort over the course of the year is used to partition the mortality into its fishing and natural components. In theory this can be done even if the tag reporting rate is unknown and estimated in the analysis. For the approach with the strong dependence on effort data we assume that fishing mortality is proportional to fishing effort over all years instead of just within a given year (i.e., that the catchability coefficient is the same for all years). There are two cases to consider. If reporting and retention–survival rates are known, then from two or more years of tag recovery data from a single release of tagged fish we can estimate natural mortality rate and the catchability coefficient (instead of estimating natural mortality and a series of individual annual fishing mortality rates). If reporting and retention–survival rates are not known, we can estimate the catchability coefficient, natural mortality rate, and the product of the tag reporting and retention–survival rates if tagged fish are released in at least 1 year and recaptures are made for at least 3 years. Alternatively, we can estimate these parameters from two or more years of recapture data when fish are tagged for each of 2 years.

The Brownie models

The structure of the Brownie models can be described in terms of the expected number of recaptures from each tagged cohort in each year (Table 1). We will assume that all animals tagged are fully recruited so that survival rate of the tagged animals does not change as the animals get older. Extension to the case of age-dependent survival rates is straightforward (Brownie et al. 1978, 1985). Suppose N_i animals are tagged in year i ($i = 1, 2, ..., I$), and of these r_{ij} are recovered in year j ($j = i, i+1, i+2, ..., J$). The quantity r_{ij} is a realization of the random variable R_{ij} representing the expected number of recaptures; the expected value, $E[R_{ij}]$, is modelled as

$$(1) \quad E[R_{ij}] = \begin{cases} N_i f_j, & i = j \\ N_i \prod_{h=i}^{j-1} S_h f_j, & j > i \end{cases}$$

where S_h is the annual survival rate for year h (probability an animal alive at the start of year h survives to the end of year h), and f_j is the tag recovery rate for year j (probability that a tagged animal alive at the start of year j is caught during year j and its tag is recovered). For convenience, let $E[R_{ij}] = N_i P_{ij}$. The recoveries for each cohort are modeled as a multinomial independent of all other cohorts. The likelihood Λ is thus

$$(2) \quad \Lambda \propto \prod_{i=1}^{I} \left(\prod_{j=i}^{J} P_{ij}^{r_{ij}} \right) P_{iJ^*}^{N_i - \sum_j r_{ij}}$$

where P_{ij} is as above for $j = i, i+1, i+2, ..., J$ and

$$(3) \quad P_{iJ^*} = 1 - \sum_{j=i}^{J} P_{ij}$$

P_{iJ^*} is the probability a tag from cohort i is not recovered (by the end of year J). Various restrictions and generalizations are possible such as assuming survival is constant over time.

For three tagged cohorts and 4 years of recaptures (Table 1), it is possible to estimate the following parameters with the basic Brownie model: f_1, f_2, f_3, S_1, S_2, and the product $S_3 f_4$. This can be seen by devising moment estimators from ratios of cell probabilities. For example,

$$\hat{f}_2 = \frac{r_{22}}{N_2}$$

$$\hat{S}_1 = \frac{N_2 r_{12}}{N_1 r_{22}} \text{ or } \frac{N_2 r_{13}}{N_1 r_{23}} \text{ or } \frac{N_2 r_{14}}{N_1 r_{24}}$$

$$\hat{S}_2 = \frac{N_3 r_{23}}{N_2 r_{33}} \text{ or } \frac{N_3 r_{24}}{N_2 r_{34}}$$

$$\widehat{S_3 f_4} = \frac{r_{34}}{N_2}$$

where the caret (^) denotes an estimate. The moment estimation approach is useful for determining what parameters are estimable, and in certain cases it leads to maximum likelihood estimators. However, in general we obtain the maximum likelihood estimates by maximizing the likelihood function.

Components of the tag recovery rate

In this paper, we assume the tag recovery rate f_j can be modeled as

$$(4) \quad f_j = \phi u_j \lambda_j$$

where ϕ is the probability that an animal survives any initial tag shedding and initial tag-induced mortality, u_j is the exploitation rate (probability that an animal present at the beginning of year j is harvested during the year) and λ_j is the tag reporting

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rate in year j (probability that the tag will be reported given that the animal is harvested in year j). Often, λ will be assumed constant over time. (Robson (1971) provided a χ^2 test for constancy of λ over time on the assumption that natural mortality is constant from year to year; however, the power of the test is not known.)

We refer to the product of the initial mortality caused by tagging and the short-term tag shedding rate as the retention–survival rate and denote this by ϕ. The retention–survival rate can be estimated by holding newly tagged animals in cages or holding pens. We will also assume that the long-term or chronic tag shedding rate is minimal. This can be verified by double tagging experiments (e.g., Hearn et al. 1991; Barrowman and Myers 1996).

The tag reporting rate can be estimated by (*i*) comparing the rate of return of tags with high-value rewards with the return rate of standard tags (Henny and Burnham 1976), (*ii*) estimating the number of tagged animals caught by a creel or port sampling survey and comparing this estimate with the number of tags voluntarily returned (Conroy 1985; Conroy et al. 1989; Pollock et al. 1991), and (*iii*) secretly placing tagged fish in fish traps or in the unprocessed catch on board fishing vessels and observing the fraction of tags returned (Costello and Allen 1968; Green et al. 1983). For completeness, we note that natural mortality and tag reporting rate can also be estimated effectively if fish are tagged before and after the fishing season each year (Hearn et al. 1998). However, as this involves a different type of study design, we do not consider this case further.

Thus, one can estimate the exploitation rate from the tag recovery rate, f, when external estimates of tag shedding, tag-induced mortality rate, and reporting rate are available. Pollock et al. (1991) showed that, if there are different tag reporting rates for different groups of fishers, then cell probabilities must be specified separately for each group. In the Appendix, we show how to incorporate the different types of reporting data into the likelihood function.

Alternatively, we show below that it is possible to estimate the product $\phi\lambda$ from the tagging data, but it appears extremely difficult to achieve meaningful levels of precision without additional information on tag reporting rate.

Instantaneous rates formulation

Fishery scientists customarily work with instantaneous rates of fishing and natural mortality, F and M, respectively. These can be derived from the exploitation rate and survival rate if the amount of fishing effort is known as a function of the time of year and the fishing mortality is assumed to be proportional to the amount of effort within periods of the year. Robson (1971) and Brownie (1974) developed a formulation for tagging models in terms of instantaneous rates, but they never published their results. Here, we present a more general formulation in which the seasonal pattern of effort can be of arbitrary form.

In year j, the exploitation rate, u_j, is a function of the fishing and natural mortality rates, which we can denote by $u_j(F_j,M_j)$ to emphasize the functional dependence. Suppose the fraction of the annual fishing effort in each period k of year j is denoted by ε_{jk}, for $k = 1, 2,..., K$ (with $\Sigma_k \varepsilon_{jk} = 1$). Let Δt be the length of a period of the year expressed as a fraction of the year. Then

$$(5a) \quad u_j = u_j(F_j,M_j) = \sum_{k=1}^{K} a_{jk}\, b_{jk}\, c_{jk}$$

where a_{jk} is the fraction of the population surviving to the beginning of period k ($a_{j1} = 1$)

$$a_{jk} = \exp(-M_j(k-1)\Delta t - F_j \sum_{h=0}^{k-1} \varepsilon_{jh}), \qquad (\varepsilon_{j0} = 0)$$

b_{jk} is the fraction dying in period k

$$b_{jk} = 1 - \exp(-M_j \Delta t - F_j\, \varepsilon_{jk})$$

and c_{jk} is the fraction of the deaths in period k due to fishing

$$c_{jk} = \frac{F_j\, \varepsilon_{jk}}{F_j\, \varepsilon_{jk} + M_j \Delta t}$$

while the annual survival rate is

$$(5b) \quad S_j = \exp(-M_j - F_j).$$

When fishing effort and hence fishing mortality are constant over the course of a year, eq. 5*a* reduces to the familiar relationship (Ricker 1975):

$$u_j(F_j,M_j) = \frac{F_j}{F_j + M_j}(1 - \exp(-F_j - M_j))$$

and when fishing occurs instantaneously at the start of the year $K = 1$, $\Delta t = 0$, $\varepsilon_{j1} = 1$, and

$$u_j(F_j) = 1 - \exp(-F_j).$$

The expected values of the number of recoveries are given in Table 2 for the case where fishing occurs at the beginning of the year (Table 2A), throughout the year with constant intensity (Table 2B), and for the general case (Table 2C). Note that these expressions will need to be adjusted if the tagging episodes are not 1 year apart, e.g., if scheduling difficulties result in intervals between tagging ranging from 10 to 14 months.

Models partitioning exploitation rate using seasonal effort data

To estimate natural and fishing mortality rates, we substitute eq. 5*a* into eq. 4, and eq. 5*b* and eq. 4 into the likelihood (eq. 2). The likelihood is maximized with respect to the parameters to obtain the maximum likelihood estimates. However, the model is overparameterized if separate fishing and natural mortalities are specified for every year. Therefore, it is necessary to specify some restrictions.

To illustrate the approach we consider two models. The first is the most general model in which F and M are allowed to vary from year to year. The second is a standard fishery model in which M is held constant while F varies. Models with various alternative restrictions on the fishing and natural mortality rates are straightforward to implement.

Model with variable F and M

For this model, the fishing and natural mortality rates are allowed to vary from year to year. However, mortality rates can only be estimated for one less than the number of years of tagging (i.e., for $I - 1$ years). The estimable parameters are

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$F_j, j = 1, 2, \ldots, I-1$
$M_j, j = 1, 2, \ldots, I-1$
f_I (or u_I)
$f_{I+1}\, S_I$
.
.
.
$f_J\, S_I\, S_{I+1} \ldots S_{J-1}$
$\phi\lambda$

Note that, for year I and beyond, it is not possible to break the exploitation rate u into its component fishing and natural mortality rates; consequently, we drop the notation $u_j(F_j, M_j)$ in favor of u_j to emphasize that the parameter is not further interpretable. The likelihood is given by eq. 2 with the P_{ij} defined by

$$P_{ij} = \begin{cases} \phi\lambda u_j\,(F_j, M_j) & i = j < I \\ \phi\lambda u_j\,(F_j, M_j) \prod_{h=i}^{j-1} e^{-F_h - M_h} & i < j < I \\ \phi\lambda u_I & i = j = I \\ \phi\lambda u_I \prod_{h=i}^{j-1} e^{-F_h - M_h} & i < j = I \\ \phi\lambda u_j\, S_I \ldots S_{j-1} & I = i < j \\ \phi\lambda u_j\, S_I \ldots S_{j-1} \prod_{h=i}^{I-1} e^{-F_h - M_h} & i < I < j \end{cases}$$

Note that the product $\phi\lambda$ is estimable in theory if $\phi\lambda$ is constant over time.

Model with variable F and constant M

Natural mortality rate is usually considered constant over time and over recruited ages in fisheries assessments. This is largely due to the difficulty until now of estimating natural mortality. Although in theory one can obtain year-specific estimates of natural mortality, it may be useful to estimate a single value to reduce the mean squared error and for comparative purposes. In this case, the parameters to be estimated are the constant mortality rate, M, and the fishing mortality in each recovery year j, $j = 1, \ldots, J$. The product $\phi\lambda$ can also be estimated if it is assumed not to vary over time. The likelihood is given by eq. 2 with P_{ij} defined as in Table 2.

In Pollock et al. (1991), the Brownie models were parameterized in terms of survival, S, and tag recovery rate, f. Thus, it was possible to estimate a separate F and M for each year (up to year $I-1$) or to estimate a single value for F and for M for all years. But, with their framework, it was not possible to impose arbitrary restrictions such as to let F vary from year to year while keeping M fixed.

Assuming catchability is constant from year to year

There is an extensive literature discussing how fishing effort is related to fishing mortality (see Hutchings and Myers 1994). When the fishing mortality is strongly related to the fishing effort, we can use the effort data to determine the relative amounts of mortality at different times and estimate the parameter (or parameters) necessary to convert from relative mortality to absolute mortality rates.

Assume that the fishing mortality, F_{jk}, in period k of year j is proportional to the effort E_{jk} in the period. Then, $F_{jk} = qE_{jk}$, where q is known as the catchability coefficient. q can be thought of as the fraction of the population caught by one unit of fishing effort when that fraction is small (say, less than 1%; Ricker 1975). The expected values of the numbers of recoveries can be derived from those given in Table 2 by replacing F_{jk} by qE_{jk} (Table 3). Then in eqs. 5*a* and 5*b*, F_j is replaced by $q\Sigma_k E_{jk}$.

When the product $\phi\lambda$ is known, the parameters q and M can be estimated from 2 years of recoveries from a single tagged cohort. For example, consider the case of a pulse fishery occurring at the beginning of each year. The expected number of recaptures in the first year is $N_1\phi\lambda(1 - e^{-qE_1})$ and the expected number in the second year is $N_1\phi\lambda(1 - e^{-qE_2})e^{-qE_1 - M}$ (Table 3). Setting the observed numbers of recaptures in the first 2 years equal to their expected values provides two equations in two unknowns, which can be solved simultaneously for M and q. Estimates of M and q can be obtained in the same way when the effort has an arbitrary distribution over the course of a year. If recoveries are obtained for more than 2 years then it is possible to estimate year-specific natural mortality rates, M_j, or to estimate more than one catchability coefficient.

If tagging is conducted for 2 years and recoveries are obtained for 2 years, the product $\phi\lambda$ is also estimable. Also, $\phi\lambda$ is estimable if tagging is conducted for 1 year and recaptures are obtained for 3 years. Consider again a pulse fishery occurring at the beginning of each year. We can solve three equations simultaneously for q, M and the product $\phi\lambda$:

$$r_{11} = N_1\phi\lambda(1 - e^{-qE_1})$$

$$r_{12} = N_1\phi\lambda(1 - e^{-qE_2})e^{-qE_1 - M}$$

$$r_{22} = N_2\phi\lambda(1 - e^{-qE_2})$$

provided $E_1 \neq E_2$. Alternatively, we can solve the system

$$r_{11} = N_1\,\phi\lambda(1 - e^{-qE_1})$$

$$r_{12} = N_1\,\phi\lambda(1 - e^{-qE_2})e^{-qE_1 - M}$$

$$r_{13} = N_1\,\phi\lambda(1 - e^{-qE_3})e^{-qE_1 - qE_2 - 2M}$$

provided not all fishing efforts are equal.

As before, the example above is easily generalized to allow for an arbitrary pattern of fishing effort over the year. The expressions for exploitation rate and survival rate in Table 3 are replaced with the appropriate modification of eqs. 5*a* and 5*b* in which F_j is replaced by qE_j.

It is a straightforward matter to allow q or M or $\phi\lambda$ to vary somewhat from year to year. For example, one might wish to try a model in which q in recent years is higher than in previous years or to explore whether q or M might have changed in years

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Table 2. Instantaneous rates formulation for expected number of tag recoveries in a multiyear tagging study when fishing mortality varies by year and natural mortality is constant over time: (A) all fishing occurs at the beginning of the year; (B) fishing occurs throughout the year with constant intensity; and (C) fishing effort follows an arbitrary pattern over the course of the year.

(A) Fishing at the beginning of the year.

	Expected recoveries in year		
Year	1	2	3
1	$N_1\phi\lambda\,(1-e^{-F_1})$	$N_1\phi\lambda(1-e^{-F_2})e^{-F_1-M}$	$N_1\phi\lambda(1-e^{-F_3})e^{-F_1-F_2-2M}$
2	—	$N_2\phi\lambda(1-e^{-F_2})$	$N_2\phi\lambda(1-e^{-F_3})e^{-F_2-M}$
3	—	—	$N_3\phi\lambda(1-e^{-F_3})$

(B) Fishing throughout the year.

	Expected recoveries in year		
Year	1	2	3
1	$\frac{N_1\phi\lambda F_1}{F_1+M}(1-e^{-F_1-M})$	$\frac{N_1\phi\lambda F_2}{F_2+M}(1-e^{-F_2-M})e^{-F_1-M}$	$\frac{N_1\phi\lambda F_3}{F_3+M}(1-e^{-F_3-M})e^{-F_1-F_2-2M}$
2	—	$\frac{N_2\phi\lambda F_2}{F_2+M}(1-e^{-F_2-M})$	$\frac{N_2\phi\lambda F_3}{F_3+M}(1-e^{-F_3-M})e^{-F_2-M}$
3	—	—	$\frac{N_3\phi\lambda F_3}{F_3+M}(1-e^{-F_3-M})$

(C) General form.

	Expected recoveries in year		
Year	1	2	3
1	$N_1\phi\lambda u_1(F_1,M)$	$N_1\phi\lambda u_2(F_2,M)e^{-F_1-M}$	$N_1\phi\lambda u_3(F_3,M)e^{-F_1-F_2-2M}$
2	—	$N_2\phi\lambda u_2(F_2,M)$	$N_2\phi\lambda u_3(F_3,M)e^{-F_2-M}$
3	—	—	$N_3\phi\lambda u_3(F_3,M)$

Note: Symbols are as follows: N_j, number tagged and released in year j; F_j, instantaneous rate of fishing mortality in year j; M, instantaneous rate of natural mortality; ϕ, probability of surviving being tagged and retaining the tag (in the short term); λ, tag reporting rate; $u_j(F_j, M)$, exploitation rate in year j as defined by eq. 5*a*. Note that u_j is a function of F_j and M and depends on the seasonal pattern of fishing.

with unusual environmental conditions. However, one cannot estimate a separate q and M for each year.

Another generalization is to allow for different types of effort, e.g., for gillnets and trawls. Then, instead of assuming $F_{jk} = q\,E_{jk}$, we have $F_{jk} = q_1\,E_{jk1} + q_2\,E_{jk2}$ when there are two types of effort. Here, the additional subscript refers to the type of effort. If the amount of the effort of the various gear types tends to vary in the same way over time, then the estimates of the qs will be highly correlated. In this case, one may need to supply an external estimate of the relative catchability of the gear types, e.g., an estimate of q_2/q_1. Then we would model the fishing mortality as

$$F_{jk} = q_1E_{jk1} + q_1(q_2/q_1)E_{jk2}$$

and we would estimate just q_1.

Using catch as a proxy for effort

It often arises that reliable effort data are not available. The data analyst then has two choices: (*i*) assume a seasonal pattern for the effort (generally, either constant over the year or concentrated at one point in the year) and check the sensitivity of the results to the assumption, or (*ii*) use the seasonal distribution of the catch as a substitute for the relative amount of effort at each point in the year. There are two ways that the seasonal distribution of catch can be determined: the total catch in the fishery can be estimated by period of the year through a creel or port sampling survey, or the number of tags recovered in a year (from all cohorts combined) can be tabulated by period of the year and used as a measure of the seasonal distribution of catch. Catch in an interval of time, C, can be modelled as a function of the effort, E, or fishing mortality, F, and the average abundance ($\bar{N}$) during the interval as follows (see Ricker 1975):

$$C = qE\bar{N} = F\bar{N}$$

Thus, if the total mortality rate during the year is not too high, the catch in each period of the year will be approximately proportional to the effort. To use catch as a substitute for effort, define the fraction of the catch in year j occurring in period k, ζ_{jk}, for $k = 1, 2, ..., K$, to be

$$(6)\qquad \zeta_{jk} = \frac{C_{jk}}{\sum_{h=i}^{K} C_{jh}}$$

The values of ζ_{jk} are then substituted for ε_{jk} in a_{jk} in eq. 5*a*.

A better approximation to the seasonal effort than eq. 6 can be obtained by adjusting the observed catches or tag returns by an approximate survival rate. This can be accomplished using

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Table 3. Expected number of tag recoveries in a multiyear tagging study when fishing mortality is assumed proportional to fishing effort and natural mortality is assumed constant: (A) all fishing occurs at the beginning of the year and (B) fishing occurs throughout the year with constant intensity.

(A) Fishing at the beginning of the year.

	Expected recoveries in year		
Year	1	2	3
1	$N_1\phi\lambda(1-e^{-qE_1})$	$N_1\phi\lambda(1-e^{-qE_2})e^{-qE_1-M}$	$N_1\phi\lambda(1-e^{-qE_1})e^{-qE_1-qE_2-2M}$
2	—	$N_2\phi\lambda(1-e^{-qE_2})$	$N_2\phi\lambda(1-e^{-qE_3})e^{-qE_2-M}$
3	—	—	$N_3\phi\lambda(1-e^{-qE_3})$

(B) Fishing throughout the year.

	Expected recoveries in year		
Year	1	2	3
1	$\frac{N_1\phi\lambda qE_1}{qE_1+M}(1-e^{-qE_1-M})$	$\frac{N_1\phi\lambda qE_2}{qE_2+M}(1-e^{-qE_2-M})e^{-qE_1-M}$	$\frac{N_1\phi\lambda qE_3}{qE_3+M}(1-e^{-qE_3-M})e^{-qE_1-qE_2-2M}$
2	—	$\frac{N_2\phi\lambda qE_2}{qE_2+M}(1-e^{-qE_2-M})$	$\frac{N_2\phi\lambda qE_3}{qE_3+M}(1-e^{-qE_3-M})e^{-qE_2-M}$
3	—	—	$\frac{N_3\phi\lambda qE_3}{qE_3+M}(1-e^{-qE_3-M})$

Note: Symbols are as follows: N_j, number tagged and released in year j; q, catchability coefficient; E_j, fishing effort in year j; M, instantaneous rate of natural mortality; ϕ, probabiliity of surviving being tagged and retaining the tag (in the short term); λ, tag reporting rate.

$$\zeta_{jk^*} = \frac{C_{jk} / \hat{S}_j^{(k-1)/K}}{\sum_{h=i}^{K} C_{jh} / \hat{S}_j^{(h-1)/K}}$$

in eq. 5*a* in place of the ε_{jk}; the estimates of S_j are obtained by maximizing eq. 2.

Even when nominal effort data are available, it may be better to use catch as the measure of effective effort. This might be the case, for example, if catchability varies substantially over the course of a year.

Example: lake trout in Cayuga Lake

Youngs and Robson (1975) presented results from a 10-year tagging study of lake trout in Cayuga Lake, New York (see Table 4). Fish were tagged in October with monel jaw tags (W.D. Youngs, personal communication). We assume the retention–survival parameter ϕ is 1.0 because the cool water temperature in autumn is not likely to stress the fish and because the jaw tag is durable.

Youngs (1974) assumed the tag reporting rate, λ, was constant over time and estimated it from the Cayuga Lake data to be 18%. For now, we will assume λ is known to be 0.18.

The timing of the fishery is not given in Youngs' papers. We analyzed the first 3 years of data under five assumptions about the timing to observe how critical it is to determine the timing. We used 3 years of data instead of 10 because 10 years of tagging data is uncommon. The assumptions were (*i*) fishing took place throughout the year with constant intensity; (*ii*) all fishing took place at the start of each year; (*iii*) all fishing took place at the end of the year; (*iv*) all fishing took place at the midpoint of the year; and (*v*) fishing took place throughout the last 6 months of the year with constant intensity during this period. Youngs has informed us (personal communication) that the fishing season extended from April through September. No information is available about the temporal pattern of effort within the 6-month fishing season. Thus, it appears that the fifth scenario most closely approximates the actual fishery.

Table 4. Tag recovery data for lake trout from Cayuga Lake, New York (from Youngs and Robson 1975).

Year	No.	Recoveries in year									
tagged	tagged	1	2	3	4	5	6	7	8	9	10
1960	1048	72	44	8	9	4	4	1	1	1	0
1961	844	—	74	30	20	7	4	2	1	0	0
1962	989	—	—	54	48	13	23	5	4	2	0
1963	971	—	—	—	74	24	16	7	3	1	1
1964	863	—	—	—	—	48	40	5	5	2	5
1965	465	—	—	—	—	—	31	10	6	3	2
1966	845	—	—	—	—	—	—	38	30	6	2
1967	360	—	—	—	—	—	—	—	19	6	6
1968	625	—	—	—	—	—	—	—	—	13	14
1969	760	—	—	—	—	—	—	—	—	—	21

We fitted two models for each assumption about timing. The first model had separate fishing mortalities in each of the 3 years and a constant natural mortality rate over the 3-year period. The second model had constant fishing and natural mortalities over the 3-year period.

The results are similar for all assumptions about timing of the fishery. The estimates of fishing mortality for year 1 range from 0.50·year^{-1} for a fishery at the beginning of the year to 0.59 for a fishery at the end of the year (Table 5). For the second year, the range of estimates is 0.64–0.74·year^{-1}, and for the third year the range is 0.40–0.45. Thus, under all five

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Table 5. Results of fitting tagging models to 3 years of lake trout recapture data.

Parameter	Estimate (SE) under fishery timing assumption				
	Continuous	Start of year	End of year	Month 7	Last 6 months
Model: year-specific F, constant M					
F_1	0.55 (0.08)	0.50 (0.08)	0.59 (0.08)	0.56 (0.08)	0.58 (0.08)
F_2	0.70 (0.09)	0.64 (0.08)	0.74 (0.11)	0.70 (0.10)	0.72 (0.10)
F_3	0.43 (0.08)	0.40 (0.06)	0.45 (0.10)	0.43 (0.08)	0.44 (0.09)
M	0.16 (0.09)	0.22 (0.11)	0.11 (0.06)	0.15 (0.08)	0.13 (0.07)
Corr(F_1,M)	–0.08	–0.38	0.15	–0.05	0.05
Corr(F_2,M)	0.43	0.12	0.59	0.47	0.53
Corr(F_3,M)	0.67	0.47	0.75	0.69	0.72
Model: constant F, constant M					
F	0.58 (0.06)	0.51 (0.04)	0.64 (0.07)	0.59 (0.06)	0.61 (0.07)
M	0.23 (0.07)	0.30 (0.09)	0.17 (0.05)	0.22 (0.07)	0.19 (0.06)
Corr(F,M)	0.44	0.11	0.56	0.45	0.52

Note: Tag reporting rate λ is assumed to be 18% and retention–survival ϕ is assumed to be 100%. Models are fitted under five different assumptions about the timing of the fishery: (1) fishing occurs with constant intensity all year; (2) pulse fishing occurs at the beginning of the year; (3) pulse fishing occurs at the end of the year; (4) pulse fishing occurs at the start of month 7; and (5) all fishing is in the last 6 months of the year and fishing intensity is constant during the fishing season. Standard errors are given in parentheses. Corr is the estimated correlation.

assumptions about timing we would come to the same qualitative conclusion that the trout population is heavily exploited. Similarly, the estimates of natural mortality under these models range from 0.11·year^{-1} for a fishery at the end of the year to 0.22 for a fishery at the beginning of the year. As previously noted, the most appropriate assumption about timing of fishing appears to be that of uniformity over the last 6 months of the year. The estimates under this assumption (last column) are close to the estimates for all other assumptions except perhaps the pulse fishery at the start of the year (second column).

For the more restricted models with fishing mortality constant over time, the estimates of F range from 0.51 to 0.64 and the estimates of M range from 0.30 to 0.17 (Table 5). Again, except for the model with all fishing occurring at the start of the year, the estimates are in close agreement.

Further sensitivity analyses and simulations

We fitted to the 10-year lake trout data set a model in which fishing mortality was allowed to vary from year to year, and natural mortality and tag reporting rate were unknown but constant over time. The retention–survival parameter ϕ was assumed to be 1.0, and fishing effort was assumed to be distributed uniformly over the year. Following Youngs (1974) we assumed that fishing occurred with constant intensity over the entire year. Our estimate, $\hat{\lambda} = 0.19$, was close to the estimate that Youngs obtained from the same data using an alternative, less efficient estimator. We then asked how reliable (stable) is this estimate. In particular, we wished to determine if reasonable estimates could be obtained with fewer than 10 years of data. We refitted the model using the first 9 years of data and also using the last 9 years of data. We then fitted the model using 8 years of data (i.e., years 1–8, 2–9, and 3–10). Continuing in this fashion, we found that the estimates are highly unstable (Fig. 1). Even with 9 years of data, the two estimates were far apart. With less than 9 years of data we frequently obtained estimates of natural mortality equal to zero. With 3 years of data the computations failed to converge twice. Therefore, it appears that the information on tag reporting rate in the data is extremely weak and additional kinds of information are required to obtain reliable estimates of reporting rate.

The computer program failed to converge when we attempted to estimate the fishing mortality rates in the first 3 years and the natural mortality rate and tag reporting rate from 3 years of recapture data from the first three tagged cohorts. We then investigated the impact on the analysis of having data from a study with high-reward tags. (We asssume the reward is so high that reporting rate for these tags is 100%.) We simulated the return of high-reward tags for the cases where 1, 2, 5, or 10% additional tags were released each year with high rewards. To generate these data, we assumed that the fishing mortalities and natural mortality in the first 3 years were equal to the estimates obtained from the full 10-year data set. We generated 500 sets of simulated tag returns for each level of additional tags.

In all cases, the computations converged though not necessarily to feasible estimates. When 1% additional tags were released with high rewards, the estimates of natural mortality rate were sometimes negative and were extremely variable (range –0.26 to 0.52) (Fig. 2). With 2% additional tags, reporting rate ranged from 0.14 to 0.32, while the estimates of natural mortality ranged from –0.06 to 0.43 year^{-1}. With 5% additional tags, the range of the estimates of reporting rate shrank to 0.16–0.27; the range of the natural mortality estimates was 0.02–0.36. With 10% additional tags, the estimates of both reporting rate and natural mortality were somewhat more precise (range for reporting rate 0.16–0.25; range for M 0.07–0.31).

Releasing 2% more tags meant that 21, 17, and 20 tags were released in the 3 years. If the tags carried a reward of $100, say, and the exploitation rate was roughly 35%, then the additional cost in terms of rewards would be about $3000 total over a 3-year period. Similar calculations for the case where 5% additional tags were released implies an added cost of rewards of $7500. Thus, it appears that the high-reward study is effective, and the cost need not be prohibitive.

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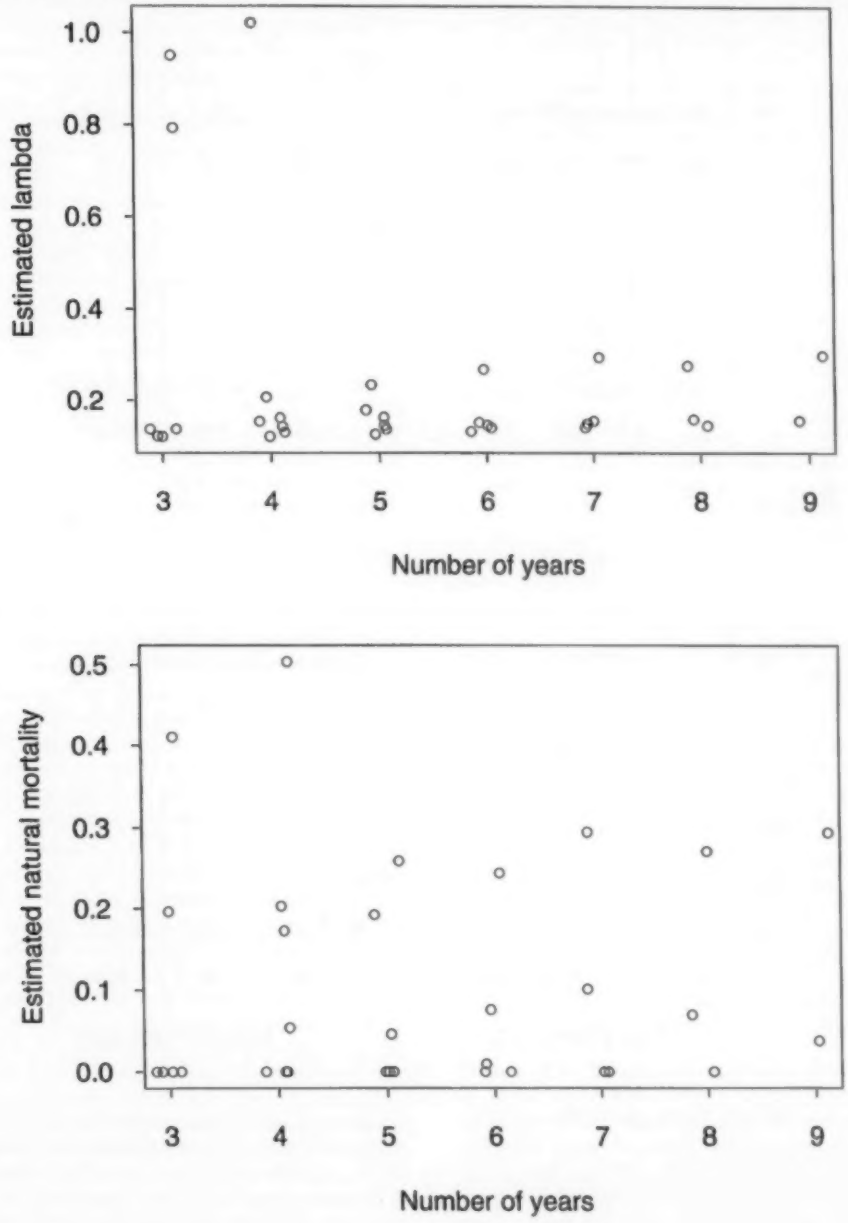
Fig. 1. Estimates of tag reporting rate, λ, (upper panel) and instantaneous natural mortality rate, M, (lower panel) for lake trout in Cayuga Lake. The abscissa gives the number of years of tagging and recovery data used. Abscissa values have been jittered (a small random number has been added to each value) to improve the readability. There are two ways to divide the 10-year data set into continuous 9-year blocks (i.e., using years 1–9 or 2–10), three ways to divide the data into 8-year blocks, etc. Note that, even with 9 years of data, the estimates are highly variable. The computer algorithm failed to converge twice when only 3 years of tagging and recovery data were considered.



Discussion

Weak assumption about effort

We have shown that information on timing of the fishery can be used to convert estimates of exploitation and survival rates into estimates of fishing and natural mortality. Fortunately, in our example it appears that estimates of mortality rates are not overly sensitive to misspecification of the timing so that even crude timing information may suffice. Because the effort data can be crude, it is even possible to use the seasonal distribution of catch (or tag recaptures) as a proxy for effort data.

The instantaneous rates formulation of the tagging models

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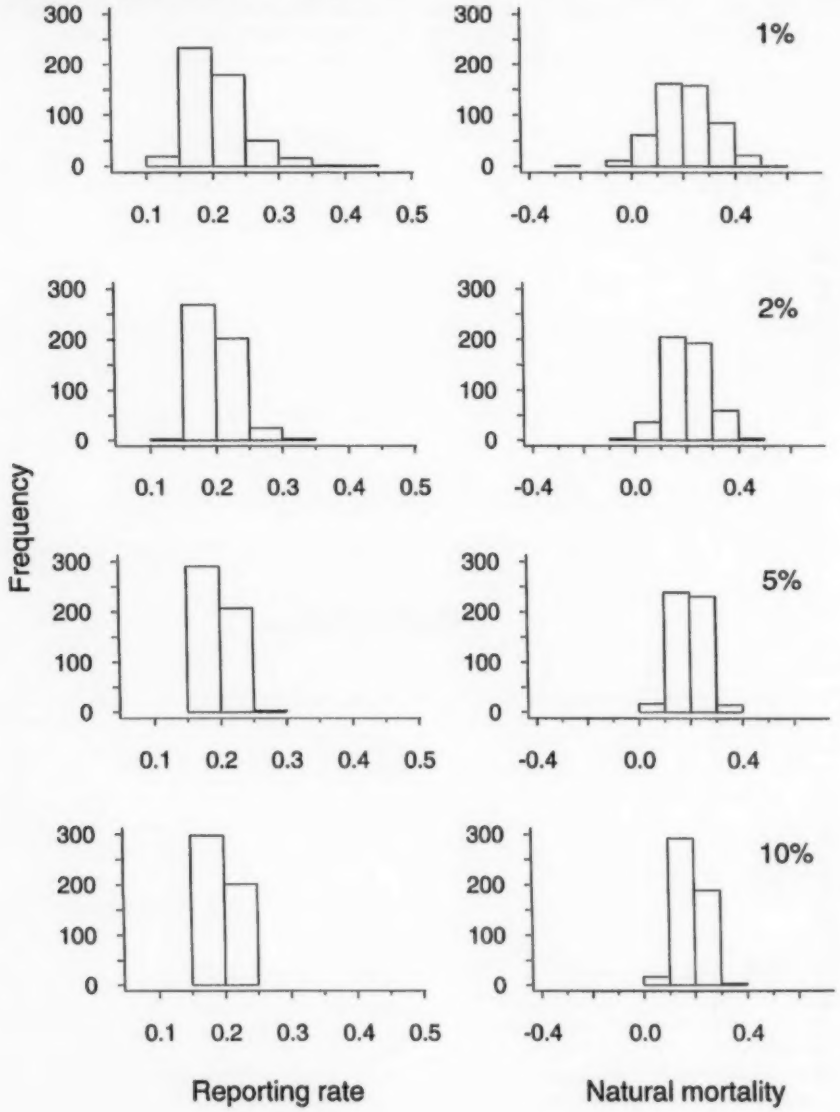
Fig. 2. Estimates of tag reporting rate (left) and natural mortality rate (right) from a 3-year tagging study (lake trout data 1960–1962) with addition of simulated returns from an additional 1% (top), 2%, 5%, or 10% (bottom) tags released each year with high rewards. Without the simulated high-reward tags, the computations failed to converge.



is important, because it allows meaningful restrictions to be imposed on the parameters such as constant natural mortality rates, separate natural mortality rates for cold and for normal years, or fishing mortality proportional to fishing effort. Formulating the tagging models in terms of instantaneous rates also bridges the gap between traditional fishery models and models of tagging data developed in the wildlife and ecological literatures. With further work, it may be possible to generalize Brownie-like tagging models to incorporate an index of abundance and the catch at age matrix.

It is clear that, in theory, the product $\phi\lambda$ can be estimated from tagging data alone (Brownie 1974; Youngs 1974). However, it appears that, in practice, it will generally be necessary to obtain additional information on tag reporting rate from a variable-reward tagging study, planted tags, or a creel or plant sampling survey (see Appendix). Our estimates of the lake trout reporting rate were not stable without additional information and Brownie's (1974) attempt to apply a version of the model to mallard duck (*Anas platyrhynchos*) data was also unsatisfactory. Fortunately, it appears that even modest numbers of tag returns with high rewards are enough to stabilize the estimate of λ (assuming ϕ is known) and thus to stabilize the estimate of M.

It is interesting that the estimates of F and M are only

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moderately correlated in the trout example and in our simulations. This suggests that it might be practical to obtain reliable estimates of natural mortality for many stocks if the study is designed carefully (see Pollock et al. 1991 for a review of the necessary assumptions). In particular, it is necessary to tag fish over the entire geographic range of the stock to ensure that the tagged population is representative of the target population, to estimate the tag-shedding and tag-induced mortality rates with cage studies, and to include a method of estimating tag reporting rate in the study.

Youngs (1974) estimated the tag reporting rate, λ, for anglers catching lake trout on Cayuga Lake from the full 10-year data set. He began by fitting his early version of what has come to be known as a Brownie model and thus estimated the annual survival rates. He then regressed the instantaneous total mortality rate Z_i ($Z_i = -\ln(S_i)$) against the tag recovery rate parameter f_i and took the reciprocal of the slope to be an estimate of the tag reporting rate. His analysis is not internally consistent, because he allowed S and f to vary freely from year to year in the first part of his analysis; however, in the second part of the analysis he assumed that λ and M were constant, and this would imply that f is a one-to-one function of S. Even though his estimator is not fully efficient, his work is notable because he clearly demonstrated that there is information about the tag reporting rate in the tagging data and he pointed the way towards parameterizing the tagging models in terms of instantaneous rates.

Strong assumption about effort

There is a large literature critical of the assumption that fishing mortality is directly proportional to fishing effort. Nonetheless, developing models based on this assumption is attractive because many fewer parameters need to be estimated. This can result in substantial improvements in precision even if some bias is introduced because of model misspecification. When the recovery matrix is sparse, it may be necessary to invoke the strong assumption about effort to make sense of the data.

Lucas (1975) developed a model for a single release of tagged animals that makes use of the strong effort assumption. He modelled the exact times of recaptures rather than the number of recaptures per interval of time. He also derived an approximate expression for the probability that an animal is not recaptured during the study. A simpler, exact expression is available, however. The principal difference between Lucas' and our approach is that Lucas implicitly assumed the tag reporting rate was 1.0, whereas we show that reporting rate can either be estimated from the tagging data, specified explicitly in the analysis, or estimated from the joint analysis of tagging and other data. It was apparently previously unrecognized that reporting rate could be estimated from a single-release tagging experiment.

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References

Barrowman, N.J., and Myers, R.A. 1996. Estimating tag shedding rates for experiments with multiple tag types. Biometrics, **52**: 1410–1416.

Brownie, C. 1974. Estimation of instantaneous mortality rates from band return data when "within-season date of kill" is also available. Biometrics Unit Mimeo Ser. Pap. No. BU-536-M Cornell University, Ithaca, N.Y.

Brownie, C., Anderson, D.R., Burnham, K.P., and Robson, D.S. 1978. Statistical inference from band recovery data—a handbook. U.S. Fish Wildl. Serv. Resour. Publ. No. 131.

Brownie, C., Anderson, D.R., Burnham, K.P., and Robson, D.S. 1985. Statistical inference from band recovery data: a handbook. 2nd ed. U.S. Fish Wildl. Serv. Resour. Publ. No. 156.

Conroy, M.J. 1985. Maximum likelihood methods for investigating reporting rates of rings of hunter-shot birds. *In* Statistics in ornithology. *Edited by* B.J.T. Morgan and P.M. North. Springer-Verlag, New York. pp. 215–241.

Conroy, M.J., Hines, J.E., and Williams, B.K. 1989. Procedures for the analysis of band-recovery data and user instructions for program MULT. U.S. Fish. Wildl. Serv. Resour. Publ. No. 175.

Costello, T.J., and Allen, D.M. 1968. Mortality rates in populations of pink shrimp, *Penaeus duorarum*, on the Sanibel and Tortugas grounds, Florida. Fish. Bull. U.S. **66**: 491–502.

Dorazio, R.M. 1992. Pre-release stratification in tag recovery models with time dependence. Can. J. Fish. Aquat. Sci. **50**: 535–541.

Green, A.W., Matlock, G.C., and Weaver, J.E. 1983. A method for directly estimating the tag-reporting rate of anglers. Trans. Am. Fish. Soc. **112**: 412–415.

Hearn, W.S., Leigh, G.M., and Beverton, R.J.H. 1991. An examination of a tag-shedding assumption, with application to southern bluefin tuna. ICES J. Mar. Sci. **48**: 41–51.

Hearn, W.S., Brooks, E., and Pollock, K.H. 1998. Pre- and post-season tagging models: estimation of reporting rate and fishing and natural mortality rates. Can. J. Fish. Aquat. Sci. **55**: 199–205.

Henny, C.J., and Burnham, K.P. 1976. A reward band study of mallards to estimate band reporting rates. J. Wildl. Manage. **40**: 1–14.

Hutchings, J.A., and Myers, R.A. 1994. What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, off Newfoundland and Labrador. Can. J. Fish. Aquat. Sci. **51**: 2126–2146.

Jagielo, T. 1991. Synthesis of mark–recapture and fishery data to estimate open-population parameters. Am. Fish. Soc. Symp. **12**: 492–506.

Larson, S.C., Saul, B., and Schleiger, S. 1991. Exploitation and survival of black crappies in three Georgia reservoirs. N. Am. J. Fish. Manage. **11**: 604–613.

Lucas, C. 1975. A method for estimating mortality rates from tag recoveries when fishing is not constant. Aust. J. Mar. Freshwater Res. **26**: 75–79.

Pollock, K.H., Hoenig, J.M., and Jones, C.M. 1991. Estimation of fishing and natural mortality when a tagging study is combined with a creel survey or port sampling. Am. Fish. Soc. Symp. **12**: 423–434.

Pollock, K.H., Tsai, K., and Hoenig, J.M. 1994. Band return models: a generalization to incorporate solicited bands and allow separation of hunting and natural mortality. J. Wildl. Manage. **58**: 193–198.

Pollock, K.H., Conroy, M.J., and Hearn, W.S. 1995. Separation of hunting and natural mortality using ring-return models: an overview. J. Appl. Stat. **22**: 557–566.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. No. 191.

Robson, D.S. 1971. Statistical analysis of reported tag-recaptures from an exploited population: maximum likelihood estimation of

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instantaneous mortality rates. Biometrics Unit Mimeo Ser. Pap. No. BU-370-M. Cornell University, Ithaca, N.Y.

Robson, D.S., and Youngs, W.D. 1971. Statistical analysis of reported tag recaptures in the harvest from an exploited population. Biometrics Unit Mimeo Ser. Pap. No. BU-369-M. Cornell University, Ithaca, N.Y.

Schwarz, C.J., Schweigert, J.F., and Arnason, A.N. 1993. Estimating migration rates using tag recovery data. Biometrics, **49**: 177–193.

Seber, G.A.F. 1970. Estimating time-specific survival and reporting rates for adult birds from band returns. Biometrika, **57**: 313–318.

Youngs, W.D. 1974. Estimation of the fraction of anglers returning tags. Trans. Am. Fish. Soc. **103**: 616–618.

Youngs, W.D., and Robson, D.S. 1975. Estimating survival rates from tag returns: model tests and sample size determination. J. Fish. Res. Board Can. **32**: 2365–2371.

Appendix. Incorporating information on tag reporting rate.

There are three basic ways to obtain information on tag reporting rate: (*i*) planted tags, (*ii*) variable (high) reward studies, and (*iii*) catch (creel or port) sampling surveys. These have been reviewed by Pollock et al. (1995).

In a planted tag study, tagged animals are placed in the catch of randomly selected fishers, and the fraction of the tags returned is taken as an estimate of the reporting rate. If each decision by a fisher on whether or not to return a tag (any tag) is made independently of the decisions for other tags then the number of planted tags reported can be taken to be a binomial random variable with parameter equal to the reporting rate in the fishery as a whole. This is closely approximated when the expected number of tag recoveries by a fisher is small (say, less than one). However, the procedure is ill defined if fishers tend not to bother returning a single tag (say, because the reward is small) but send in tags when several have accumulated.

On the assumption that returns of planted tags follow a binomial distribution, then if x tags are returned out of n planted, the likelihood for the planted tag data is

$$\text{(A1)}\quad \Lambda_p = \binom{n}{x}\lambda^x (1-\lambda)^{n-x}$$

where λ is the tag reporting rate. The likelihood (eq. 2) for regular tags is multiplied by the likelihood (eq. A1) for planted tags to get the joint likelihood for both types of data.

In a high reward tag study, a number of tagged animals are released with messages that clearly indicate the tags can be returned for a high reward. A publicity campaign is conducted so that the fishing community is aware of these high-reward tags. The assumption is made that the rewards are sufficiently high and the publicity campaign is sufficiently extensive that the tags from 100% of the recaptured animals are reported. The reporting rate for standard tags can be estimated as the ratio of the proportion of returns of standard to high-reward tags.

The expected value of the number of returns from the ith release of high-reward tags captured in year j is exactly the same as for standard tags (e.g., in Table 2) except that everywhere that λ occurs it is replaced by 1.0. Thus, the likelihood for the high reward tag data is constructed in exactly the same way as for the standard-tag data (except for the λ) and the joint likelihood for both types of data is the product of the two likelihoods.

When a port sampling or creel survey is conducted, there are two types of tag returns: those that are solicited directly by the survey agent from the fishers and those that are voluntarily returned by fishers who have not encountered a survey agent. The former are assumed to be surrendered or reported with probability 1.0, while the latter are reported with probability λ. If δ is the fraction of the fishery that is surveyed (e.g., δ = 0.10 if 20% of the access points are surveyed on 50% of the days of the fishing season) then 100δ% of the tags from recaptured fish are expected to be recovered from the survey, leaving $100(1-\delta)$% of the tags to be voluntarily reported with probability λ. Thus, we again have two sets of expected values. For solicited tags, the expected number of returns from year j ($j \geq i$) is

$$E_s(R_{ij}) = N_i f_{js} \prod_{h=i}^{j-1} S_h = N_i u_j \delta_j \prod_{h=i}^{j-1} S_h$$

while for tags reported without solicitation the expected value is

$$E_r(R_{ij}) = N_i f_{jr} \prod_{h=i}^{j-1} S_h = N_i u_j (1-\delta_j) \prod_{h=i}^{j-1} S_h$$

where ΠS_h is defined to be 1.0 if $j = i$. The tags recovered by solicitation and by voluntary reporting (as well as those never recovered) together form one multinomial distribution for each year of tagging.

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Models for tagging data that allow for incomplete mixing of newly tagged animals

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Abstract: The Brownie models for tagging data allow one to estimate age- and year-specific total survival rates as well as tag recovery rate parameters. The latter can provide estimates of exploitation rates if the tag reporting, tag shedding, and tag-induced mortality rates can be estimated. A limitation of the models is that they do not allow for newly tagged animals to have different survival rates than previously tagged animals because of lack of complete mixing. We develop a model that allows for the animals to be incompletely mixed, or not fully recruited, into the population during the entire year in which they are tagged. There is a penalty in terms of precision associated with the use of this model. To increase the precision, we also developed a model for which it is assumed that animals become fully mixed (recruited) after a portion of the year has elapsed. Sometimes, animals must be tagged after the fishing season has begun. In this case, newly tagged animals experience fishing and natural mortality for only a fraction of the year. The partial-year non-mixing model can be modified to account for this situation.

Résumé : Les modèles de Brownie pour les données de marquage permettent d'évaluer le taux de survie totale propre à un âge et à une année ainsi que des paramètres du taux de récupération des marques. Ces derniers peuvent fournir des évaluations du taux d'exploitation lorsqu'on peut estimer les taux de déclaration des marques, de perte des marques et de mortalité induite par les marques. Le fait que dans ces modèles les sujets nouvellement marqués ne peuvent pas avoir des taux de survie différents de ceux des animaux déjà marqués en raison d'un mélange incomplet constitue une limitation. Nous avons élaboré un modèle qui permet un mélange incomplet des animaux, ou un recrutement incomplet, dans la population pendant toute l'année au cours de laquelle ils ont été marqués. L'utilisation de ce modèle comporte un désavantage au niveau de la précision. Afin d'accroître la précision, nous avons également élaboré un modèle dans le cadre duquel on suppose que les poissons sont entièrement mélangés (recrutés) après un certain temps. Les poissons doivent être parfois marqués après le début de la saison de pêche. Dans ce cas, ces poissons nouvellement marqués ne sont exposés à une mortalité par pêche et à une mortalité naturelle que pendant une partie de l'année. Le modèle de non-mélange pendant une partie de l'année peut être modifié pour prendre en compte cette situation.
[Traduit par la Rédaction]

Introduction

Brownie et al. (1978, 1985) developed simple, elegant and generally robust models for data from multiyear tagging studies. These models allow one to estimate year-specific survival rates and rates of tag recovery. The latter were originally viewed as nuisance parameters, because they represented the combined effects of tag-induced mortality, tag shedding, exploitation, and tag reporting. In recent years, it has been recognized that tag-induced mortality and tag shedding could be quantified by holding tagged animals in cages or pens. Also, tag reporting rate could be estimated from planted tags, creel or port sampling programs, or high-reward tagging studies. Thus, it is possible to determine the exploitation rate from the tag recovery rate (Conroy 1985; Conroy et al. 1989; Pollock et al. 1991, 1994, 1995).

One limitation of the Brownie models, pointed out by Youngs and Robson (1975), is that it is necessary to assume that newly tagged animals have time to mix thoroughly among the previously tagged animals before the fishing season begins and that they are fully recruited. This can be difficult to achieve in practice. Youngs and Robson developed a test for non-mixing but were unable to remedy the problem in the context of Brownie models.

Hoenig et al. (1998) reparameterized the Brownie models in terms of instantaneous rates of fishing and natural mortality. Here, we show that the instantaneous rates formulation makes it possible to allow for non-mixing (and incomplete recruitment) of newly tagged animals. We develop two kinds of models: those in which the newly tagged animals are mixed through the population after 1 year and those in which the animals are mixed after a fraction of the year has passed.

Instantaneous rates formulation of the Brownie models

Consider a tagging study where animals are tagged at the start of each year and animals are recaptured over a number of years

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Table 1. Instantaneous rates formulation for expected number of tag recoveries in a multiyear tagging study.

	Expected recoveries in year		
Year	1	2	3
1	$N_1\phi\lambda u_1(F_1,M)$	$N_1\phi\lambda u_2(F_2,M)e^{-F_1-M}$	$N_1\phi\lambda u_3(F_3,M)e^{-F_1-F_2-2M}$
2	—	$N_2\phi\lambda u_2(F_2,M)$	$N_2\phi\lambda u_3(F_3,M)e^{-F_2-M}$
3	—	—	$N_3\phi\lambda u_3(F_3,M)$

Note: Symbols are as follows: N_i, number tagged and released in year i; F_j, instantaneous rate of fishing mortality in year j; M, instantaneous rate of natural mortality; ϕ, probabiliity of surviving being tagged and retaining the tag (in the short term); λ, tag reporting rate; $u_j(F_j,M)$, exploitation rate in year j as defined by eq. 1 (note that u_j is a function of F_j and M and depends on the seasonal pattern of fishing).

with the animals being killed upon recapture. Let N_i be the number of animals tagged in year i for $i = 1, 2,..., I$, and let r_{ij} be the number of animals tagged in year i and recaptured in year j for $j = i, i + 1, i + 2,..., J$. The observed numbers of recaptures r_{ij} are realizations of the random variables R_{ij} whose expected values are shown in Table 1 for a model in which the instantaneous fishing mortality rate, F_j, is year-specific and the instantaneous natural mortality rate, M, is constant over time. In Table 1, ϕ is the probability an animal survives the tagging process with the tag intact, λ is the tag reporting rate (probability the tag is reported given that a tagged fish is caught), and $u_j(F_j,M)$ is the exploitation rate in year j. The expected value of R_{11} can be interpreted as follows: of the N_1 fish tagged in year 1, the fraction ϕ of the fish will survive the tagging with the tag in place; of these, the fraction $u_1(F_1,M)$ will be caught, with a fraction λ of these reported. The expected value of R_{12} has a similar interpretation: $N_1\phi$ fish are available to be caught at the start of year 1, of these the fraction $\exp(-F_1 - M)$ survives the first year and is available to be caught in the second year, and of these the fraction $\lambda u_2(F_2,M)$ is caught and reported during the second year. Expected values for all cells in the table can be constructed in like fashion.

The exploitation rate, $u_j(F_j,M)$, is a function of the fishing and natural mortality rates. It depends on the relative timing of the components of mortality. We will assume that the natural mortality rate occurs with constant intensity over the course of a year. Suppose the fraction of the annual fishing effort in each period k of year j is denoted by εjk, for $k = 1, 2, ..., K$. We assume that the fraction of the fishing mortality occurring in period k is equal to the fraction of the annual fishing effort occurring in period k (see Hoenig et al. 1998). Let Δt_k be the length of the kth period of the year expressed as a fraction of the year. Then

$$(1) \qquad u_j(F_j,M) = \sum_{k=1}^{K} a_{jk} b_{jk} c_{jk}$$

where a_{jk} is the fraction of the population surviving to the beginning of period k, with $a_{j1} = 1$ and

$$a_{jk} = \exp\left(-M\sum_{h=1}^{k-1}\Delta t_h - F_j\sum_{h=1}^{k-1}\varepsilon_{jh}\right), \qquad k > 1$$

b_{jk} is the fraction dying in period k

$$b_{jk} = 1 - \exp(-M\Delta t_k - F_j\,\varepsilon_{jk})$$

and c_{jk} is the fraction of the deaths in period k due to fishing

$$c_{jk} = \frac{F_j\,\varepsilon_{jk}}{F_j\,\varepsilon_{jk} + M\Delta t_k}$$

When fishing effort and hence fishing mortality are constant over the course of a year (eq. 1) reduces to the familiar relationship (Ricker 1975):

$$u_j(F_j,M) = \frac{F_j}{F_j + M}(1 - \exp(-F_j - M))$$

and when fishing occurs instantaneously at the start of the year $K = 1$, $\Delta t_1 = 0$, $\varepsilon_{j1} = 1$, and

$$u_j(F_j) = 1 - \exp(-F_j).$$

The right-hand side of eq. 1 can be substituted for $u_j(F_j,M)$ in the expressions for the expected values. Then the models for the tagging data are parameterized in terms of instantaneous rates of fishing and natural mortality, tag reporting rate, and tag retention–survival (ϕ). Hoenig et al. (1998) discuss how reporting rate and tag retention–survival can be estimated, and they show how the likelihood function can be constructed to obtain maximum likelihood estimates. The models discussed in this paper can be fitted using program SURVIV (White 1983).

Table 2. Instantaneous rates formulation for expected number of tag recoveries in a multiyear tagging study when newly tagged animals are not fully mixed into the population in the year of tagging.

	Expected recoveries in year		
Year	1	2	3
1	$N_1\phi\lambda u_1(F_1^*,M)$	$N_1\phi\lambda u_2(F_2,M)e^{-F_1^*-M}$	$N_1\phi\lambda u_3(F_3,M)e^{-F_1^*-F_2-2M}$
2	—	$N_2\phi\lambda u_2(F_2^*,M)$	$N_2\phi\lambda u_3(F_3,M)e^{-F_2^*-M}$
3	—	—	$N_3\phi\lambda u_3(F_3^*,M)$

Note: Symbols are as follows: N_j, number tagged and released in year j; F_j, instantaneous rate of fishing mortality in year j for previously tagged animals; F_j^*, instantaneous rate of fishing mortality in year j for newly tagged animals; M, instantaneous rate of natural mortality; ϕ, probability of surviving being tagged and retaining the tag (in the short term); λ, tag reporting rate; $u_j(F_j,M)$, exploitation rate (for previously tagged animals) in year j as defined by eq. 1 (note that u_j is a function of F_j and M and depends on the seasonal pattern of fishing); $u_j(F_j^*,M)$, exploitation rate for newly tagged animals in year j.

Models that allow for non-mixing

Non-mixing in the year of tagging

Now suppose that the newly tagged animals do not mix throughout the tagged population immediately upon release. Then, in general, the newly tagged animals would be expected to experience a different fishing mortality rate than the previously tagged animals. In Table 2 we describe a model in which this is the case.

The expression for the expected value of r_{11} indicates that the newly tagged animals experience fishing mortality F_1^*. Throughout this paper we use an asterisk to indicate parameters referring to newly tagged animals that are not yet fully mixed into the population. We make the assumption that the

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relative timing of the fishing and natural mortality on the newly tagged animals is the same as before. However, this is not a critical assumption, because we are not interested in the value of the fishing mortality on newly tagged animals (since it does not reflect what is happening to the population at large), and because the relative timing has a minor effect on the estimates of mortality rates (see Hoenig et al. 1998).

The expected number of recaptures in year 2 from animals tagged in year 1 depends in part on the fishing mortality experienced by the cohort in year 1 and also on the "normal" fishing mortality, F_2, experienced by fully mixed animals in year 2:

$$E[R_{12}] = N_1\phi\lambda u_2(F_2,M)e^{-F_1^*-M}$$

In the above, $\exp(-F_1^* - M)$ is the survival rate in year 1 of newly tagged animals, while $u_2(F_2,M)$ is the exploitation rate in year 2 of animals tagged prior to year 2. Note that the recapture of newly tagged animals in year 2 has expected value:

$$E[R_{22}] = N_2\phi\lambda u_2(F_2^*,M)$$

That is, these animals experience a different fishing mortality rate (F_2^*) than the previously tagged animals (which experience rate F_2).

The tag recoveries from the 2 years of tagging and 3 years of recapture are modelled with six parameters: F_1^*, F_2^*, F_2, F_3, M, and the product $\phi\lambda$. If the product $\phi\lambda$ is known from external information, then setting the observed recaptures (r_{11}, r_{12}, r_{13}, r_{22}, r_{23}) equal to their expected values provides five equations in five unknowns, which can be solved simultaneously to obtain moment estimates of the parameters. If a fourth year of recaptures is obtained then there are two more observations (r_{14} and r_{24}) but only one additional parameter (F_4). In this case, it is possible in theory to also estimate F_4 and the product $\phi\lambda$. With additional tag releases or years of recapture it is possible to estimate additional parameters, e.g., letting natural mortality or the product $\phi\lambda$ vary to some extent over time. It is not possible, however, to estimate a separate fishing mortality rate and natural mortality rate for every year (excluding the first year) even if the product $\phi\lambda$ is known.

Although it is theoretically possible to estimate a wide variety of parameters, in practice it is necessary to introduce restrictions such as holding natural mortality constant to obtain stable estimates (see section on simulation results).

Non-mixing during part of the year of tagging

From the expected values in Table 2, it is clear that the recapture of newly tagged animals provides no information about fishing mortality on previously tagged animals. Thus, the assumption of a non-mixing model results in the loss of a great deal of information. It is therefore of interest to see if some information about fishing mortality rates for previously tagged animals can be obtained from the recapture of newly tagged animals. We do this by assuming that after a portion of the year has passed the animals are fully mixed.

Suppose that fishing effort data are collected by period of the year and, for the first w periods, the newly tagged animals are not mixed into the population. Then for w periods the newly tagged animals will experience an abnormal fishing mortality rate and for $K - w$ periods they will experience the normal fishing mortality rate, i.e., the same rate experienced by the previously tagged animals. The survival rate, S_j^*, of newly tagged animals in year j can thus be expressed by

$$S_j^* = \exp\left(-F_j^*\sum_{k=1}^{w}\Delta t_k - F_j\sum_{k=w+1}^{K}\varepsilon_{jk} - M\right)$$

where F_j^* now refers to the fishing mortality on newly tagged animals during the first w periods of year j. (The summation over Δt_k serves only to express F_j^* per year; the summation over ε_{jk} applies only a fraction of the normal fishing mortality to the newly tagged animals.) Similarly, the exploitation rate for newly tagged animals in year j can be expressed as

$$(2)\qquad u_j^*(F_j^*,F_j,M) = b_j^*c_j^* + \sum_{k=w+1}^{K}a_{jk}^*b_{jk}c_{jk}$$

For the first part of the year, b_j^* is the fraction dying

$$b_j^* = 1 - \exp\left(-(M + F_j^*)\sum_{k=1}^{w}\Delta t_k\right)$$

and c_j^* is the fraction of the deaths due to fishing

$$c_j^* = \frac{F_j^*}{F_j^* + M}$$

For the second part of the year (periods $w + 1, 2, \ldots, K$), the fraction surviving to the beginning of period k is

$$a_{jk}^* = \begin{cases} \exp\left(-M\sum_{h=1}^{k-1}\Delta t_h - F_j^*\sum_{h=1}^{k-1}\Delta t_h\right), & k = w+1 \\ \exp\left(-M\sum_{h=1}^{k-1}\Delta t_h - F_j^*\sum_{h=1}^{w}\Delta t_h - F_j\sum_{h=w+1}^{k-1}\varepsilon_{jh}\right), & k > w+1 \end{cases}$$

This just adds up the natural mortality since the beginning of the year, the abnormal fishing mortality F_j^*, and the portion of the normal fishing mortality that has occurred up to the beginning of the kth period.

In a competing risks model such as this, it is assumed implicitly that the ratio of fishing to natural mortality rate on unmixed animals is constant over the first w periods and within each period after that. Although this assumption is not likely to be met in the first part of the year, the results are not sensitive to the relative timing of the fishing and natural mortalities (see Hoenig et al. 1998).

For the first year of tagging, the above expression for survival (S_1^*) introduces two parameters — F_1 and F_1^*. However, there is little basis for distinguishing between these parameters. Therefore, we model the survival rate in the first year by

$$S_1^* = \exp(-F_1^* - M)$$

to eliminate the parameter F_1. Similarly, we can eliminate F_1 from the expression for exploitation rate in the first year by replacing eq. 2 with

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Table 3. Recapture data from a tagging study of lake trout (*S. namaycush*) described by Youngs and Robson (1975).

Year	No. tagged	No. recaptured in year 1	2	3	4	5
1960	1048	72	44	8	9	4
1961	844	—	74	30	20	7
1962	989	—	—	54	48	13
1963	971	—	—	—	74	24
1964	863	—	—	—	—	48

$$u_1^*(F_1^*,M) = \sum_{k=1}^{K} a_{1k}^* b_{1k}^* c_{1k}^*$$

where the factors are the same as in eq. 1 except that F_1 is replaced by F_1^*. In other words, we treat the data from the first year of the tagging study as if animals are not completely mixed into the population until an entire year has elapsed. In this case, we lose the ability to estimate F_1, but our ability to do this was poor anyway.

Tagging after the fishing season begins

An interesting situation is where animals are tagged after the fishing season has begun. This is not really a non-mixing model, but it can be handled in a fashion similar to that used for non-mixing. Suppose all tagging is done in a short period of time w periods after the season begins, and tagged animals are released throughout the area inhabited by the stock. Then it might be reasonable to assume that animals are thoroughly mixed as soon as they are released. In this case, the fishing and natural mortality rates on newly tagged animals would be 0 during the first w periods of the year and would be the same as for previously tagged animals for all other periods of the year. Thus, the annual survival rate for the newly tagged animals would be

$$S_j^* = \exp\left(-F_j \sum_{k=w+1}^{K} \varepsilon_{jk} - M \sum_{k=w+1}^{K} \Delta t_k\right), \quad j = 1, 2, ..., I$$

and the exploitation rate would be

$$u_j^*(F_j,M) = \sum_{k=w+1}^{K} a_{jk}^{**} b_{jk} c_{jk}, \quad j = 1, 2, ..., I$$

with all symbols defined as for eq. 1 except $a_{j,w+1}^{**} = 1$ and

$$a_{jk}^{**} = \exp\left(-M \sum_{h=w+1}^{k-1} \Delta t_h - F_j \sum_{h=w+1}^{k-1} \varepsilon_{jh}\right), \quad k > w+1.$$

Tests for non-mixing

We can use a likelihood ratio test to compare the fits of a model assuming complete mixing to one allowing for non-mixing of newly tagged animals. Let Λ_m and Λ_n be the values of the likelihood functions for the models assuming complete mixing and non-mixing, respectively, evaluated at the parameter estimates. (The model assuming non-mixing is the "full" model while the model assuming complete mixing is the "restricted" model). Then, under the null hypothesis that the fully mixed (restricted) model is true, the expression

$$-2 \log_e\left(\frac{\Lambda_m}{\Lambda_n}\right)$$

has an asymptotic χ^2 distribution with degrees of freedom Δ equal to the difference in the number of parameters estimated under the two models. The fully mixed model is rejected in favor of the non-mixed model if the value of the test statistic exceeds the critical value for a χ^2 variable with Δ degrees of freedom.

Table 4. Two model fits to the data in Table 3.

Parameter	Estimate	SE
Fully mixed model		
F_1	0.58	0.08
F_2	0.69	0.07
F_3	0.42	0.05
F_4	0.65	0.07
F_5	0.40	0.07
M	0.11	0.04
Non-mixed model		
F_1^*	0.59	0.08
F_2^*	0.64	0.09
F_3^*	0.41	0.07
F_4^*	0.63	0.11
F_5^*	0.41	0.08
F_2	0.82	0.18
F_3	0.45	0.10
F_4	0.68	0.16
F_5	0.40	0.14
M	0.11	0.05

Note: The fully mixed model assumes newly tagged animals are fully mixed into the population. Negative log likelihood = 2101.1; χ^2 goodness of fit statistic = 8.13 with 9 df, $p = 0.52$. The non-mixed model assumes a lack of mixing in the year of tagging. Negative log likelihood = 2100.3; χ^2 statistic = 6.54 with 5 df, $p = 0.26$.

Example: lake trout in Cayuga Lake

We consider 5 years of results from a tagging study described by Youngs and Robson (1975) of lake trout (*Salvelinus namaycush*) in Cayuga Lake, New York (Table 3). Youngs (1974) estimated the tag reporting rate, λ, from these data to be 18%. (Actually, the estimate is of the product $\phi\lambda$.) Hoenig et al. (1998) showed that the estimate was not stable. Therefore, for illustrative purposes, we will assume that the product $\phi\lambda$ is known to be 0.18, and we will not try to estimate $\phi\lambda$. The fishing season occurred during the last 6 months of the year, assuming the year begins in October when the animals were tagged (W.D. Youngs, personal communication).

We fitted two models to the data, one which allowed for non-mixing throughout all of the year of tagging (non-mixed model) and one which was based on the assumption that animals were fully mixed throughout all of the year of tagging (fully mixed model). In both models, the fishing mortality was allowed to vary from year to year, natural mortality was held constant, fishing effort was assumed to be of constant intensity

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Table 5. Tagging data from Table 3 modified to simulate lack of mixing in the year of tagging.

Year	No. tagged	No. recaptured in year 1	2	3	4	5
1960	1048	48	55	10	11	5
1961	844	—	49	39	26	9
1962	989	—	—	36	56	15
1963	971	—	—	—	49	31
1964	863	—	—	—	—	32

Note: Recaptures of newly tagged animals (along the main diagonal) were reduced by one-third to simulate an exploitation rate on newly tagged animals that is two-thirds that of previously tagged animals. Recaptures in subsequent years were increased to reflect the higher survival of animals in their year of tagging (see text for details).

during months 7 to 12 of the year, and the product $\phi\lambda$ was fixed at 0.18.

Both models fit the data well judging by the χ^2 goodness of fit statistics. The estimates from the two models were very similar (Table 4). Both models provided estimates of M of around 0.11·year^{-1} and both models indicated that the fishing mortality rates were quite high. The estimated standard errors for the non-mixed model were noticeably higher than for the fully mixed model.

To see how the models might perform in a case where non-mixing is a problem, we modified the data set to simulate a non-mixing scenario. The numbers of recaptures along the main diagonal of the recapture matrix were multiplied by two-thirds to simulate newly tagged animals having an exploitation rate two-thirds that of previously tagged animals. This meant that the number of recaptures in subsequent years had to be adjusted upwards to account for the higher survival rate in the year of tagging. This adjustment was accomplished as follows. The natural mortality rate and fishing mortality rates estimated from the original data (assuming a fully mixed population) were used to calculate the exploitation rate in the year of tagging for each cohort. We then searched iteratively for the fishing mortality rate F^* that would result in the exploitation rate being reduced to two-thirds of the original value. Every entry in a row to the right of the cell for newly tagged animals was then multiplied by the ratio of the survival rates (new:old), i.e., by $\exp(F_i - F_i^*)$ where F_i is the fishing mortality that occurred on the newly tagged animals from cohort i (in year i) and F_i^* is the fishing mortality that would have resulted in two-thirds the exploitation rate. The results were rounded to the nearest whole number (Table 5).

The fit of the fully mixed model to the data modified to reflect non-mixing was extremely poor (Table 6). The chi-square goodness of fit statistic was highly significant suggesting the model was not appropriate, and there was a clear pattern to the residuals: the residuals were all negative on the main diagonal and positive immediately to the right of the main diagonal. The χ^2 statistic suggests the non-mixed model fit well, and there was no obvious pattern to the residuals (Table 6). The estimated fishing mortality rates for previously tagged animals, and the estimated natural mortality rate, were similar to those obtained when the mixing model was fitted to the original data. Thus, it appears that the non-mixed model successfully handled the non-mixing situation.

Table 6. Model fits to the data in Table 5.

Parameter	Estimate	SE
Fully mixed model		
F_1	0.33	0.05
F_2	0.47	0.05
F_3	0.29	0.04
F_4	0.42	0.06
F_5	0.26	0.05
M	0.05	0.05
Non-mixed model		
F_1^*	0.36	0.06
F_2^*	0.38	0.06
F_3^*	0.25	0.05
F_4^*	0.37	0.07
F_5^*	0.25	0.06
F_2	0.82	0.14
F_3	0.46	0.08
F_4	0.69	0.16
F_5	0.41	0.13
M	0.12	0.05

Note: Data were modified from Table 3 to represent an exploitation rate on newly tagged animals that is two-thirds that of previously tagged animals. For the fully mixed model, negative log likelihood = 1985.3; χ^2 goodness of fit = 34.45, 9 df, $p < 0.0001$. For the non-mixed model, negative log likelihood = 1972.7; $\chi^2 = 7.62$, 5 df, $p = 0.18$.

Simulation studies

We conducted a simulation study of a tagging program with 3 years of tagging and 3 years of recaptures to see how well models assuming complete mixing and assuming non-mixing in the first year performed under a variety of situations. In particular, we wished to see how great is the penalty for having to assume a non-mixed model. This is important inasmuch as the extent of non-mixing problems may be controlled by the choice of time for tagging.

We simulated the following conditions:

(1) a type I (pulse) or type II (continuous) fishery;
(2) number tagged per year was 500 or 1000;
(3) $\phi = 1$ and reporting rate (λ) was 1.0 or 0.50, assumed known;
(4) fishing mortality for fully mixed animals was constant at either $F = 0.2$·year^{-1} or $F = 0.4$·year^{-1};
(5) natural mortality rate was constant at either 0.2·year^{-1} or 0.4·year^{-1}; and
(6) fishing mortality on newly tagged animals (F^*) was either (*i*) the same as for previously tagged animals, (*ii*) 0.1 when $F = 0.2$, or (*iii*) 0.3 when $F = 0.4$.

We fitted models that either assumed constant fishing and natural mortality rates or just constant natural mortality. We fitted non-mixed models to data generated with non-mixing, and we fitted fully mixed models to data generated as fully mixed.

For each set of conditions, we generated 1000 data sets. Results for each estimated parameter were summarized by computing the bias and the relative standard error. The bias is defined to be the average of the 1000 estimates minus the true value of the parameter. For a parameter θ, estimated by $\hat{\theta}$, the bias is $\text{bias}(\hat{\theta}) = \overline{\hat{\theta}} - \theta$, where $\overline{\hat{\theta}}$ is the average of the

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Table 7. Results of simulations to determine relative standard errors (%) of estimated mortality rates.

	$F = 0.2$				$F = 0.4$			
	$M = 0.2$		$M = 0.4$		$M = 0.2$		$M = 0.4$	
Parameter	$F^* = F$, mixed	$F^* = 0.1$, non-mixed	$F^* = F$, mixed	$F^* = 0.1$, non-mixed	$F^* = F$, mixed	$F^* = 0.3$, non-mixed	$F^* = F$, mixed	$F^* = 0.3$, non-mixed
Year-specific mortality assumed								
F_1^*	—	10.19	—	10.19	—	6.19	—	6.19
F_2^*	—	10.15	—	10.14	—	6.18	—	6.18
F_3^*	—	10.20	—	10.20	—	6.20	—	6.20
F_1	7.40	—	7.40	—	5.50	—	5.50	—
F_2	6.10	14.47	6.31	16.89	4.67	11.02	4.81	12.94
F_3	6.59	18.66	6.72	21.65	4.99	14.44	5.10	17.04
M	24.84	52.65	14.15	31.66	18.00	35.61	10.62	22.03
Constant mortality assumed								
F^*	—	5.88	—	5.88	—	3.57	—	3.57
F	4.10	14.45	4.15	16.88	3.06	10.95	3.09	12.90
M	22.50	46.59	13.08	28.26	16.67	31.63	10.00	19.61

Note: Animals were tagged for 3 years and recaptured for 3 years. Mortality rates were held constant over time. Estimates were made separately under two assumptions, either that (*i*) natural mortality is constant over time but fishing mortalities vary over time (top), or (*ii*) mortality rates are constant over time (bottom). In half of the simulations, newly tagged animals have the same fishing mortality as previously tagged animals while, in the other half, the fishing mortality on newly tagged animals is less than that on previously tagged ones. Non-mixed models were fitted to data sets in which newly and previously tagged animals had different mortality rates. Type 1 (pulse) fishery (N =1000 tagged/year; $\phi\lambda$= 100%).

1000 estimates. The relative standard error is defined to be the standard error of $\hat{\theta}$ divided by θ. It is computed as

$$\text{Relative SE}(\hat{\theta}) = \frac{\left(\dfrac{\sum_{i=1}^{1000}(\hat{\theta}_i - \bar{\theta})^2}{999}\right)^{1/2}}{\theta}$$

where $\hat{\theta}_i$ is the parameter estimate for the ith simulated data set.

In all cases, the biases were small so we restricted our attention to the relative standard errors. Results for the pulse fishery case with N = 1000 animals tagged per year and $\phi\lambda$ = 100% are shown in Table 7. Qualitatively, the results in this table are the same as for all other simulated conditions: there is a significant penalty for having to assume a non-mixed model. Typically, the standard error for a parameter estimated under a non-mixed model is greater than that for the corresponding parameter under a fully mixed model by a factor of two to three. The effect of halving the number of animals tagged is approximately the same as halving the reporting rate. Both serve to reduce the expected number of tag returns and to increase the relative standard errors by approximately 50%. If a continuous (type II) fishery is simulated, the estimated fishing mortalities have slightly higher relative standard errors, and the estimated natural mortality rate(s) has (have) slightly lower relative standard error(s), than if a pulse (type I) fishery is simulated; however, these differences are so small as to be of little practical significance.

Discussion

It is reasonable to assume that the lake trout data considered in the example represent a case where the newly tagged animals are fully mixed into the population when the fishery begins each year. This is because tagging takes place approximately 6 months before the fishery begins. Analysis of the data reveals that a model based on the assumption of complete mixing fits the data very well. Fitting a non-mixed model to these data results in similar estimates to those obtained under the fully mixed model. However, the standard errors are noticeably larger for the non-mixed model.

When we modified the data to simulate a non-mixed situation with abnormally low fishing mortality on the newly tagged animals, the model assuming full mixing performed extremely poorly (low χ^2 goodness of fit statistic, pattern to the residuals, and estimated mortality rates substantially different than those estimated from the original data). In contrast, the non-mixed model performed very well. The model fit the data well judging by the χ^2 statistic and the lack of pattern to the residuals. Furthermore, the estimated natural mortality rates and the fishing mortality rates on previously tagged animals were close to those estimated from the original data.

The simulation results confirm that there is a substantial penalty for having to use a non-mixed model. Insofar as possible, the person designing a tagging program should endeavor to minimize the non-mixing problem by choice of suitable times and locations for the tagging. Apart from that, the options for dealing with non-mixing are to increase the number of recaptures by increasing the number of animals tagged, increase the number of recaptures by increasing the tag reporting rate (e.g., by increasing the reward for returning a tag), or use a model that assumes the period of non-mixing lasts for less than a whole year.

This is the first paper to propose a solution to the non-mixing problem. Brownie et al. (1978, 1985) proposed a model (model 0), which allows for newly tagged animals to have a different tag reporting rate than previously tagged animals but the same exploitation rate and survival rate. They pointed out that if newly tagged animals have a different exploitation rate (and hence different survival rate) than previously tagged animals, the model would be indistinguishable

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from their model 0. However, the parameters that can be estimated with model 0 do not include the annual survival rates. That is, the survival rates are confounded with the tag recovery rate parameters so that one can only estimate products of parameters that are not interesting. Our models allow one to estimate fishing and natural mortality rate and thus annual survival rate.

It appears feasible, if expensive, to deal with non-mixing. Further analytical efforts in this area may result in further gains. For example, Hearn et al. (1998) recently described a tagging study design in which animals are tagged before and after the fishery. This provides direct estimates of natural mortality that can be compared with the natural mortality estimated from the kind of data considered here; significant non-mixing would cause a discrepancy in the estimates.

In this paper, we consider the case where there is one count of recaptures per cohort per year. In some cases, it may be possible to apportion the total recaptures from a cohort to subannual periods. For example, it may be possible to determine how many of the recaptures occurred in the first half of the year and how many in the second half by using follow-up interviews of the fishers. This would provide a class of models intermediate between the Brownie-like models and exact time of recapture models (see Hearn 1986; Hearn et al. 1987). The likelihood would still be multinomial, but there would be two cells per year. As before, one would determine an expression for the expected value for each cell of the recovery matrix and raise the expected value to the observed number in the cell. In addition to increasing the precision of the estimates, this type of model would also enable one to estimate the fishing mortality (F_1) in the first year of the study.

References

Brownie, C., Anderson, D.R., Burnham, K.P., and Robson, D.S. 1978. Statistical inference from band recovery data—a handbook. U.S. Fish and Wildl. Serv. Resour. Publ. No. 131.

Brownie, C., Anderson, D.R., Burnham, K.P., and Robson, D.S. 1985. Statistical inference from band recovery data: a handbook. 2nd ed. U.S. Fish and Wildl. Serv. Resour. Publ. No. 156.

Conroy, M.J. 1985. Maximum likelihood methods for investigating reporting rates of rings of hunter-shot birds. *In* Statistics in ornithology. *Edited by* B.J.T. Morgan, and P.M. North. Springer-Verlag, New York. pp. 215–241.

Conroy, M.J., Hines, J.E., and Williams, B.K. 1989. Procedures for the analysis of band-recovery data and user instructions for program MULT. U.S. Fish. Wildl. Serv. Res. Publ. No. 175.

Hearn, W.S. 1986. Mathematical methods for evaluating marine fisheries. Ph.D. dissertation, School of Zoology, University of New South Wales, Kensington, Australia.

Hearn, W.S., Pollock, K.H., and Brooks, E. 1998. Pre- and post-season tagging models: estimation of reporting rate and fishing and natural mortality rates. Can. J. Fish. Aquat. Sci. **55**: 199–205.

Hearn, W.S., Sandland, R.L., and Hampton, J. 1987. Robust estimation of the natural mortality rate in a completed tagging experiment with variable fishing intensity. J. Cons. Cons. Int. Explor. Mer, **43**: 107–117.

Hoenig, J.M., Barrowman, N.J., Hearn, W.S., and Pollock, K.P. 1998. Multiyear tagging studies incorporating fishing effort data. Can. J. Fish. Aquat. Sci. **55**. This issue.

Pollock, K.H., Hoenig, J.M., and Jones, C.M. 1991. Estimation of fishing and natural mortality when a tagging study is combined with a creel survey or port sampling. Am. Fish. Soc. Symp. **12**: 423–434.

Pollock, K.H., Tsai, K., and Hoenig, J.M. 1994. Band return models: a generalization to incorporate solicited bands and allow separation of hunting and natural mortality. J. Wildl. Manage. **58**: 193–198.

Pollock, K.H., Conroy, M.J., and Hearn, W.S. 1995. Separation of hunting and natural mortality using ring-return models: an overview. J. Appl. Stat. **22**: 557–566.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. No. 191.

White, G.C. 1983. Numerical estimation of survival rates from band-recovery and biotelemetry data. J. Wildl. Manage. **47**: 717–728.

Youngs, W.D. 1974. Estimation of the fraction of anglers returning tags. Trans. Am. Fish. Soc. **103**: 616–618.

Youngs, W.D., and Robson, D.S. 1975. Estimating survival rates from tag returns: model tests and sample size determination. J. Fish. Res. Board Can. **32**: 2365–2371.

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Use of passive integrated transponder tags to estimate survival of migrant juvenile salmonids in the Snake and Columbia rivers

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Abstract: Single-release and modified single-release statistical models were evaluated as means to generate reliable survival estimates from release–recapture studies of migrant salmonid smolts in the Snake and Columbia rivers of the northwestern United States. Monte Carlo simulation studies were used to assess robustness of estimation methods to violations of model assumptions. To field test model assumptions, passive integrated transponder tagged chinook salmon (*Oncorhynchus tshawytscha*) smolts were released on seven consecutive days in 1993 above Lower Granite Dam on the Snake River. These releases were used to estimate sampling variability of survival estimates for comparison with model-based variance estimates and to assess mixing of detected and nondetected individuals. Field results satisfied model assumptions. The average survival estimate from point of release to the tailrace of Lower Granite Dam (31 km) was 0.902 ± 0.004 (mean ± SE). From the tailrace of Lower Granite Dam to the tailrace of Little Goose Dam (60 km) the average survival estimate was 0.859 ± 0.013.

Résumé : On a évalué l'efficacité de modèles statistiques de lâcher simple et de lâcher simple modifié pour produire des estimations fiables de la survie à partir d'études de lâcher–recapture de smolts en migration dans la rivière Snake et le fleuve Columbia, dans le nord-ouest des États-Unis. On s'est servi de la méthode de Monte Carlo pour évaluer la robustesse des méthodes d'estimation dans les cas où les hypothèses du modèle ne sont pas respectées. Afin de mettre ces hypothèses à l'essai sur le terrain, des saumons quinnats (*Oncorhynchus tshawytscha*) étiquetés à l'aide d'une marque transpondeur intégré passif ont été libérés pendant 7 jours consécutifs en 1993 en amont du barrage Lower Granite, sur la rivière Snake. On s'est servi de ces lâchers pour estimer la variabilité due à l'échantillonnage dans les estimations de la survie afin de les comparer aux estimations de la variance fondées sur le modèle et d'évaluer le mélange des individus détectés et non détectés. Les résultats obtenus sur le terrain correspondaient aux hypothèses du modèle. L'estimation de la survie moyenne entre le point de lâcher et le canal de fuite du barrage Lower Granite (31 km) était 0,902 ± 0,004 (moyenne ± ET). Entre le canal de fuite du barrage Lower Granite et celui du barrage Little Goose (60 km), l'estimation de la survie moyenne était 0,859 ± 0,013. [Traduit par la Rédaction]

Introduction

In the middle to late 1980s, the National Marine Fisheries Service (NMFS) developed a miniature passive integrated transponder (PIT) tag that, when implanted in the body cavity of juvenile fish, allows for unique identification of individuals (Prentice et al. 1990*a*, 1990*b*, 1990*c*). For migrant juvenile salmonids PIT-tagged in the Snake River Basin, detectors automatically decode the tags as fish pass through juvenile fish collection facilities at selected hydroelectric dams (Fig. 1).

In 1988, the University of Washington (UW) began to develop statistical theory and software to estimate survival probabilities and assess survival relationships from data generated by release and detection of PIT-tagged fish in the Snake and Columbia rivers. From this work was developed the statistical software SURPH.1 (Smith et al. 1994) used in the studies described herein. In 1993, these technologies came together in a joint NMFS–UW pilot study of smolt survival in the Snake River (Iwamoto et al. 1994). This collaboration of electronic technology, statistical theory, and fisheries biology to devise an effective system for information gathering and analysis is a first in the science of animal-tagging studies.

This paper describes the statistical models used to analyze survival studies with PIT-tagged fish, their assumptions, sampling precision, and robustness to model violations. Further, we describe the field methods used in 1993 to collect, PIT-tag, and release migrant juvenile salmonids in the Snake River to gather data for the models. Monte Carlo simulation results are presented, along with the results of seven replicate releases in 1993, to determine the validity of the estimation procedures. The PIT-tag studies in 1993 also provided some of the first survival estimates for juvenile chinook salmon (*Oncorhynchus tshawytscha*) in the Snake River since a summary of survival estimates in the 1970s was made by Sims and Ossiander (1981). We discuss extension of these technologies to the investigation, mitigation, and recovery of salmonid stocks in the Snake–Columbia River Basin.

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Fig. 1. Study area showing release and detection sites.

Materials and methods

Field methods

Study area

PIT-tagged fish were released in Lower Granite Reservoir near Nisqually John boat landing (river kilometer (Rkm) 726), at Lower Granite Dam (Rkm 695), and at Little Goose Dam (Rkm 635) on the Snake River in Washington State. PIT-tagged fish were detected at Lower Granite Dam, Little Goose Dam, and Lower Monumental Dam (Rkm 589) on the Snake River and at McNary Dam (Rkm 470) on the Columbia River (Fig. 1). Lower Granite and Little Goose dams also had facilities to return PIT-tagged fish detected in the bypass systems back into the river in the tailrace (Fig. 2).

Survey design

The primary objective of the field study was to estimate smolt survival from Nisqually John boat landing to the tailrace of Lower Granite Dam ($\hat{S}_1$) and survival from the tailrace of Lower Granite Dam to the tailrace of Little Goose Dam ($\hat{S}_2$). A secondary objective was to estimate survival from the point of detection in the bypass system to the point in the tailrace at each dam where detected fish remixed with nondetected fish ($\hat{\tau}_2$,$\hat{\tau}_3$) (Fig. 2). Primary release groups (R_1) consisted of hatchery-reared yearling chinook salmon captured by purse seine in Lower Granite Reservoir and PIT-tagged near the Nisqually John boat landing (Fig. 2). There was one primary release per day for seven consecutive days. Daily releases ranged from 797 to 1405 tagged fish, depending on availability. Capture histories from each group were the basis for estimating survival in the river sections above Little Goose Dam (Table 1).

Secondary, paired releases of PIT-tagged fish were made at Lower Granite (R_{B2}, C_{B2}) and Little Goose Dams (R_{B3}, C_{B3}) to investigate potential mortality of fish returned to the river after detection. If such mortality occurs in the bypass system, it could bias estimates of reach survival obtained from the primary releases. Test groups were released in the bypass system at the juvenile collection facilities, just downstream from the PIT-tag detector. Control groups were released in the river below the dam at a point where bypassed fish remixed with fish that passed via turbines or spillways. Each paired release was replicated three times at each dam (Table 2).

Release and detection data were transmitted to the PIT-tag information system (PTAGIS) for later retrieval and analysis. PTAGIS is a computer database developed for the Columbia River Basin and managed by the Pacific States Marine Fisheries Commission (PIT Tag Operations Center, 45 SE 82nd Drive, Suite 100, Gladstone, OR 97207, U.S.A.).

Fish collection and handling

For the primary release groups in Lower Granite Reservoir, fish were collected using two purse-seine vessels (Durkin and Park 1967). Purse seines were approximately 229 m long and 11 m deep with 1- to 2-cm webbing (stretch measure). Effective fishing depth was about 6 m. Seines were towed upstream in a U shape for 10–30 min prior to pursing. For the secondary releases, fish were obtained from the juvenile collection facilities at the respective dams.

Only hatchery-reared yearling chinook salmon, determined by the absence of either adipose or ventral fins (clipped at hatchery), were used in this study. Fish with extreme injuries, excessive descaling, or obvious bacterial kidney disease (BKD) symptoms were excluded, as were previously PIT-tagged fish (identified by scanning with a PIT-tag detector). During sorting and marking, fish were kept anesthetized with tricaine methanesulfonate (MS-222) in a recirculating anesthetic system at a dosage of approximately 50 ppm.

Fish were PIT-tagged using modified hypodermic syringes containing a push rod, terminal air hole, and 12-gauge needle (Prentice et al. 1990c; Nielsen 1992). The PIT-tag needle was inserted alongside the midventral line between the ventral and pelvic fins, and the tag was placed into the body cavity posterior to the pyloric caeca (Prentice et al. 1990c). Studies that have looked at the effects of PIT-tagging on salmon smolt growth or survival have found no significant effects (Prentice et al. 1987, 1990*a*; Prentice 1990). The small entry wound tends to heal quickly.

Smolts used in the primary releases (i.e., R_1) were kept in net-pens (1.8 × 0.9 × 0.7 m) for 32–54 h prior to release. Mortalities were

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removed, scanned, and recorded prior to release. Smolts used to estimate post-detection bypass mortality were held in aluminum tanks with flow-through water at the dams. These smolts were generally held for at least 24 h prior to release with all mortalities recorded and counts adjusted accordingly.

Detection of PIT-tagged fish

At each dam, a variety of passage routes were available for migrating smolt. Fish could either pass over the spillway or enter the powerhouse (passage through navigation locks is negligible). The powerhouses of each dam were equipped with screening devices to guide fish away from turbine intakes and into "juvenile bypass systems," that have historically been used to collect fish to be transported downstream in barges or trucks. Not all fish were successfully guided and consequently some passed through turbines. PIT-tag detectors were installed only in the juvenile bypass systems. As a PIT-tagged fish passed through a detector, the tag code was recorded automatically (the fish was not handled). At Lower Granite and Little Goose Dams, the PIT-tag detector triggered a "slide gate" to divert the fish away from the transportation collection facilities and back into the river. However, not all detected fish were successfully diverted back to the river. Nondiverted fish were transported, and their capture histories were subsequently censored at that point.

Statistical methods

Single-release (SR) model

Survival probabilities through a section of a river or reservoir can be estimated using a single release of tagged fish upstream with multiple detection sites downstream. The minimal design configuration is an upstream release site and two downstream detection sites with the uppermost detection facility capable of returning detected fish to the river. In 1993, the Snake–Columbia River study used four detection sites. The two uppermost sites (Lower Granite and Little Goose dams) had both detection and rerelease capabilities and the two lower sites (Lower Monumental and McNary dams) had only detection and removal capabilities. For purposes of data analysis, detections at Lower Monumental and McNary Dams were not differentiated. The single release–recapture (SR) model was first presented by Cormack (1964), Jolly (1965), and Seber (1965). This model is also a special case of paired-release models using complete capture histories introduced, but not fully developed in its own right, by Burnham et al. (1987). The single release–recapture design is a special case of designs that can readily be analyzed using the interactive computer program SURPH.1 (Smith et al. 1994).

The likelihood model (SR model) for each single release of the 1993 Snake River survival study can be written as follows:

$$(1)\quad L(\underset{\sim}{S},\underset{\sim}{p},\lambda|\underset{\sim}{R},\underset{\sim}{m}_1,\underset{\sim}{m}_2,\underset{\sim}{m}_3) =$$

$$\begin{aligned}
&\binom{R_1}{m_{12},m_{13},m_{14}}(S_1p_2)^{m_{12}}(S_1(1-p_2)S_2p_3)^{m_{13}}\\
&\times(S_1(1-p_2)S_2(1-p_3)\lambda)^{m_{14}}\\
&\times(1-S_1(p_2+(1-p_2)\lambda+(1-p_2)S_2(1-p_3)\lambda))^{R_1-r_1}\\
&\times\binom{R_2}{m_{23},m_{24}}(S_2p_3)^{m_{23}}(S_2(1-p_3)\lambda)^{m_{24}}\\
&\times(1-S_2(p_3+(1-p_3)\lambda))^{R_2-r_2}\binom{R_3}{m_{34}}\lambda^{m_{34}}(1-\lambda)^{R_3-r_3}
\end{aligned}$$

where R_1 is the number of PIT-tagged fish released above Lower Granite Dam; R_2 is the number of PIT-tagged fish detected and released at Lower Granite Dam; R_3 is the number of PIT-tagged fish detected and rereleased at Little Goose Dam; m_{ij} is the number of fish released at the ith site ($i = 1, 2, 3$) first detected at the jth detection site ($j = i+1,..., 4$); $r_i = \Sigma_{j=i+1}^{4} m_{ij}$, for $i = 1, 2, 3$; S_1 is the survival probability from point of release to tailrace of Lower Granite Dam; S_2 is the survival probability from Lower Granite tailrace to tailrace of Little Goose Dam; p_1 is the detection probability at Lower Granite Dam; p_2 is the detection probability at Little Goose Dam; and λ is the joint probability of surviving from tailrace of Little Goose Dam and being detected at either Lower Monumental Dam or McNary Dam.

Fig. 2. Schematic of release locations, detection, and slide-gate rerelease facilities used to estimate survival (S), capture rates (p), and post-detection survival (τ).

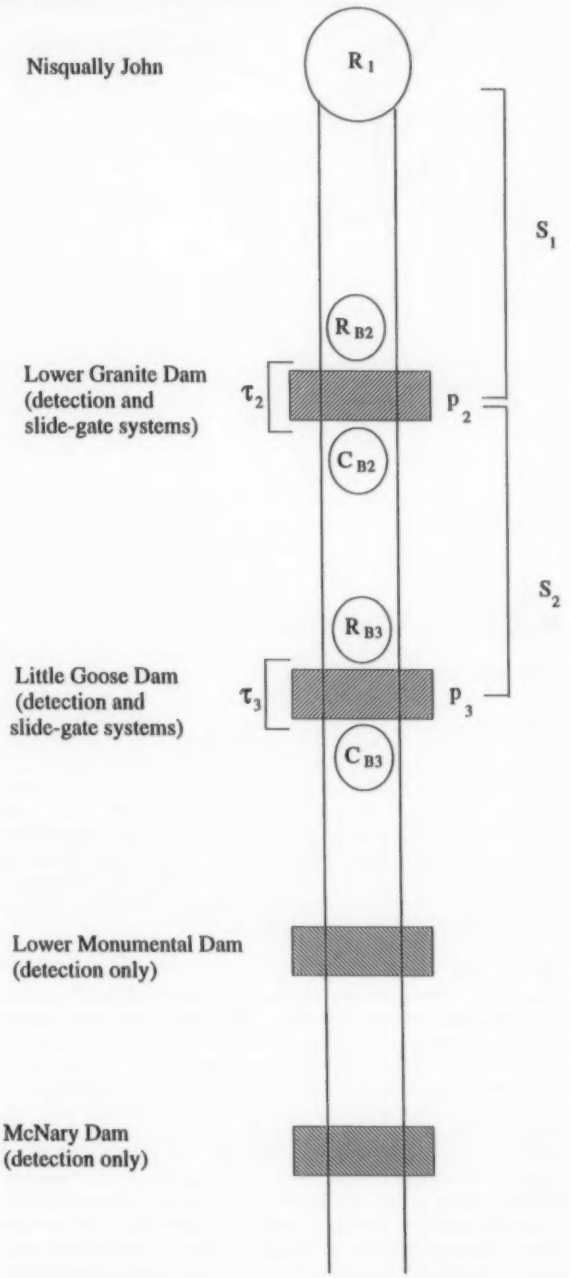

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Table 1. Number of fish in each primary release group and their associated capture histories (0, not detected; 1, detected and released; 2, detected and removed).

Capture history	Release group and date						
	R_{11} 15 April	R_{12} 16 April	R_{13} 17 April	R_{14} 18 April	R_{15} 19 April	R_{16} 20 April	R_{17} 21 April
1 1 1	66	118	91	74	75	52	96
0 1 1	111	146	128	120	86	69	97
1 0 1	81	119	100	106	107	82	130
0 0 1	129	142	132	160	136	109	171
1 1 0	46	52	33	42	33	28	53
0 1 0	70	93	66	48	50	36	80
1 0 0	87	110	103	114	115	67	156
0 0 0	223	280	259	296	260	177	351
2 0 0	148	174	171	182	204	133	226
0 2 0	54	71	69	66	47	44	45
1 2 0	30	44	36	27	29	23	43
Total	1015	1305	1152	1208	1113	797	1405

Table 2. Number of fish released (i.e., R_{B2} and C_{B2} or R_{B3} and C_{B3}) and subsequent capture histories for each pair of replicate releases (0, not detected; 1, detected and released; 2, detected and removed).

(A) Lower Granite Dam.

Capture history	28 April		30 April		12 May	
	R_{B2}	C_{B2}	R_{B2}	C_{B2}	R_{B2}	C_{B2}
1 1	132	155	107	152	15	20
0 1	155	189	193	189	137	129
1 0	79	85	99	82	65	81
0 0	287	263	250	260	525	501
2 0	75	68	47	59	6	12
Total	728	760	696	742	748	743

(B) Little Goose Dam.

Capture history	7 May		8 May		13 May	
	R_{B3}	C_{B3}	R_{B3}	C_{B3}	R_{B3}	C_{B3}
1	273	413	452	423	117	98
0	186	279	285	307	634	637
Total	459	692	737	730	751	735

When all fish detected at a dam are rereleased (i.e., $R_2 = m_{12}$, $R_3 = m_{13} + m_{23}$), the statistical model can be simplified.

Formulae for the parameter estimates are simplified by defining the following variables:

$$m_j = \sum_{i=1}^{j-1} m_{ij}, \qquad \text{for } j = 2 \text{ and } 3$$

$$z_j = \sum_{i=1}^{j-1} \sum_{k=j+1}^{4} m_{ij}, \qquad \text{for } j = 2 \text{ and } 3$$

$$T_j = m_j + z_j, \qquad \text{for } j = 2 \text{ and } 3$$

The parameter estimates and associated variances can be written as follows:

(2) $$\hat{S}_1 = \frac{r_1}{R_1}\left(\frac{m_2}{T_2} + \frac{z_2 R_2}{T_2 r_2}\right)$$

with

(3) $$\widehat{\mathrm{var}}(\hat{S}_1|S_1) = (\hat{S}_1)^2\left[\frac{1}{r_1} - \frac{1}{R_1} + (1-p_2)^2\left(\frac{1}{r_2} - \frac{1}{R_2}\right)\right] + (\hat{S}_1)^2(1-p_2)^2\left(1 - \frac{r_2}{R_2}\right)^2 \frac{m_2}{z_2 T_2}$$

(4) $$\hat{S}_2 = \frac{r_2}{R_2}\left(\frac{m_3}{T_3} + \frac{z_3 R_3}{T_3 r_3}\right)$$

with

(5) $$\widehat{\mathrm{var}}(\hat{S}_2|S_2) = (\hat{S}_2)^2\left[\frac{1}{r_2} - \frac{1}{R_2} + (1-p_3)^2\left(\frac{1}{r_3} - \frac{1}{R_3}\right)\right] + (\hat{S}_2)^2(1-p_3)^2\left(1 - \frac{r_3}{R_3}\right)^2 \frac{m_3}{z_3 T_3}$$

while

(6) $$\hat{p}_2 = \frac{m_2}{m_2 + z_2 R_2 / r_2}$$

(7) $$\hat{p}_3 = \frac{m_3}{m_3 + z_3 R_3 / r_3}$$

and

(8) $$\hat{\lambda} = \frac{r_3}{R_3}$$

These estimators were first derived by Cormack (1964) and later by Burnham et al. (1987, pp. 112–116). Approximate 95% confidence interval estimates for survival probabilities (S_k) can be calculated according to the formula:

(9) $$95\%\ \mathrm{CI} = \hat{S}_k \pm 1.96\,(\widehat{\mathrm{var}}(\hat{S}_k|S_k))^{1/2}$$

Although we used the standard formula (eq. 9), normality assumptions could be avoided by using profile likelihood methods (Hudson 1971).

Assumptions associated with the SR model are as follows:

(A1) The test fish are representative of the population of inference.
(A2) Test conditions are representative of the conditions of interest.
(A3) The number of fish released is exactly known.
(A4) PIT-tag codes are accurately recorded at the time of tagging and at all detection sites.
(A5) For replicated studies, data from different releases are statistically independent.

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(A6) The fate of each individual fish is independent of the fates of all other fish.
(A7) All fish in a release group have equal survival and detection probabilities.
(A8) Prior detection history has no effect on subsequent survival and detection probabilities.

Assumptions A1–A5 are pertinent for the validity of statistical inferences to the population of interest and to the proper conduct of the study. These assumptions (i.e., A1–A5) are largely satisfied by appropriate capture, handling, marking, and release procedures of the study protocol. Postrelease handling mortality could violate assumption A1 and tend to underestimate actual survival probabilities. Careful handling is therefore needed to avoid such bias and was the reason fish were held at least 24 h prior to release.

The key assumptions in constructing the multinomial likelihood (eq. 1) are A6–A8, which imply that the fates (i.e., capture histories) of all PIT-tagged fish in a release group are independent, identically distributed, multiple Bernoulli trials. Assumptions A6–A8 are mathematical constraints in the formulation of likelihood (eq. 1), and investigators have less direct control over them than assumptions A1–A5. For this reason, these assumptions warrant closer scrutiny. In the sections that follow, we first describe the effects of various violations of assumptions A6–A8 on survival estimates and associated variance estimates from the SR model. We then present a series of data analyses that were performed to test whether the assumptions were satisfied in the 1993 Snake River survival study.

Monte Carlo simulations

Heterogeneity in survival probabilities among the fish within a release group can violate assumption A7. Monte Carlo simulation studies were used to evaluate the robustness of the SR model to three forms of survival heterogeneity. The first potential violation of assumption A7 can be stated as follows:

(V7a) Survival probabilities for individual smolts are heterogeneous because of inherent differences in viability of fish.

To evaluate the robustness of the model in eq. 1 to violation V7a, Monte Carlo simulations were conducted, each consisting of 1000 fish released above Lower Granite Dam. A total of 1000 simulations were conducted for each scenario investigated. Detection probabilities were 0.50, 0.55, and 0.60 at Lower Granite, Little Goose, and McNary dams, respectively. The distribution of survival probabilities among individual smolts depended on the distribution of a condition index. Each fish was assigned a standardized condition index from a normal distribution with mean (μ) = 0 and standard deviation (σ) = 0.1 for convenience. Heterogeneous survival probabilities among individual smolts were created by assuming a proportional hazards relationship based on the condition index. In terms of survival probabilities, a smolt with condition index x was assigned survival probabilities $S_1 = S_{10}^{e^{-2x}}$, $S_2 = S_{20}^{e^{-2x}}$, and $S_3 = S_{30}^{e^{-2x}}$ from release to Lower Granite, Lower Granite to Little Goose, and Little Goose to Lower Monumental, respectively. Two scenarios were investigated. In scenario V7a.1, the baseline survival (i.e., S_{10}) probability was 0.88 for all three reaches. In scenario V7a.2, the baseline survival probabilities were $S_{10} = 0.6$, $S_{20} = 0.9$, and $S_{30} = 0.5$. In both scenarios, 20% of detected fish were removed for barging downstream at each dam. Program SURPH.1 (Smith et al. 1994) can relax assumption A7 by permitting the survival and detection probabilities of individual fish to be modeled as functions of individual-based covariates. Individual-based models will not be explored in this analysis (see Skalski et al. 1993; Smith et al. 1994).

The second potential violation of A7 can be stated as follows:

(V7b) Survival probabilities for individual smolts are heterogeneous because survival rates differ among the various routes through the hydroelectric projects (i.e., spill, bypass, turbines).

Risks of mortality are not the same in each of the passage routes through a dam. For the simulated scenarios, survival probabilities were calculated as the product of two independent probabilities. The first component was survival from the top of the reach to the forebay of the next downstream dam (i.e., the "pool"). This survival probability was set at 0.95. The second component of survival was the probability of surviving dam passage. Survival through the dam depended on whether passage occurred through the spillbays (S_{spill}), turbines ($S_{turbine}$), or bypass system (S_{bypass}). In this set of simulations, mortality in the bypass system occurred before detection. The proportion of fish going through the alternative routes was allowed to vary (Table 3). In all V7b scenarios, of those fish entering the powerhouse (not the spill), the proportion passing through the bypass system (i.e., fish guidance efficiency (FGE)) was 0.45, 0.50, and 0.55 at Lower Granite, Little Goose, and McNary dams, respectively. In all scenarios, 20% of detected fish at each dam were removed for barging downstream (i.e., right censored).

Table 3. Passage route-specific survival rates for scenarios simulated under violation V7b.

Scenario	Probability through spill	Survival probabilities		
		S_{spill}	S_{bypass}	$S_{turbine}$
V7b.1	0.2	0.90	0.90	0.90
V7b.2	0.6	0.90	0.90	0.90
V7b.3	0.2	0.97	0.98	0.85
V7b.4	0.6	0.97	0.98	0.85
V7b.5	0.2	0.80	0.50	0.30
V7b.6	0.6	0.80	0.50	0.30

Note: Release sizes of 1000 PIT-tagged fish were simulated 1000 times under each scenario.

A potential violation of assumption A8 can be stated as follows:

(V8) Survival probabilities for individual smolts are heterogeneous because the route taken through a hydroelectric project affects downstream survival (or detection) probabilities.

Currently, PIT-tagged fish can be detected only in the juvenile bypass facilities of the dams. Consequently, detected fish traverse a different part of the tailrace than fish that pass via turbines or spillway. Assumption A8 would be violated if the subsequent level of mortality experienced by detected fish differs from that experienced by nondetected fish. For example, such a difference could be caused by differential predation mortality in the tailrace between fish passing through the bypass system and those using other passage routes, prior to remixing below the dam. The parameters for scenarios under violation V8 were identical to those under V7b (Table 3), except that mortality in the bypass system occurred after detection and before remixing with nondetected fish at Lower Granite and Little Goose Dams.

Tests of assumptions based on field trials

The validity of assumption A8 was evaluated using three distinct approaches. If two or more groups of tagged fish are mixed as they travel down the river, they will experience the same river and dam passage conditions. Thus, mixing of distinct groups is a sufficient, but not necessary, condition for equal capture and survival probabilities. The hypothesis that groups are mixed can be tested by comparing distributions of daily detections at downstream dams, using Pearson χ^2 tests of homogeneity based on contingency tables (Snedecor and Cochran 1989, pp. 210 and 211). The first test of assumption A8 was a comparison of the distributions of daily detections at downstream sites for subgroups of primary releases defined by their upstream capture history. Contingency table entries for Little Goose Dam distributions were the number of fish detected each day from two subgroups of each release: those detected at Lower Granite Dam, and those not detected at Lower Granite Dam. Similar tests of homogeneity were based on daily tag detections at Lower Monumental Dam for four subgroups defined by capture histories at Lower Granite and Little Goose dams.

The second method for testing assumption A8 was presented by

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Burnham et al. (1987) and called TEST 3. This test checked the internal consistency of survival and capture probabilities by dividing a single release group into subgroups based on their capture histories up to a specified location. The two detection and diversion sites followed by two detection-only sites provided sufficient data to construct one contingency table analysis under TEST 3.

Each series of contingency table tests (one test for each of seven primary releases) was considered to be a single experiment, and significance levels were selected to control the experimentwise type I error rate at $\alpha_{EX} = 0.05$. With seven tests in each experiment, the testwise significance level was $\alpha_T = 0.0073$.

A third approach to testing assumption A8 was based on data from the secondary paired releases and is presented in the next section.

If the fates of individual fish are not independent (i.e., assumption A6 violated), point estimates of survival and detection probabilities for a release group remain valid and unbiased. However, model-based variance estimates tend to underestimate true variability under nonindependence. To determine whether the likelihood model (eq. 1) provided an accurate estimate of the variance of the survival estimates (eqs. 3 and 5), the seven primary releases in Lower Granite Reservoir were clustered in time as closely as possible. As such, the variability in the respective point estimates of survival should be almost exclusively the result of sampling variability and not because of changing survival probabilities associated with varying river conditions. The empirical variance among the seven point estimates (i.e., s_S^2) was compared with the average variance estimated from the model (i.e., $\overline{\widehat{\mathrm{Var}}(\hat{S}_i|S_i)}$). There was no formal test of significance. However, if the empirical variance was much greater than the average variance predicted by the model, this would imply that the model was not accounting for a substantial source of variability.

Modified single-release (MSR) model

Assumption A8 is violated if fish detected in the juvenile fish bypass facility experience differential mortality before remixing with fish that passed though turbines or spillways. Data from the secondary paired releases at Lower Granite and Little Goose Dams, in conjunction with a modification of the SR model (eq. 1), can be used to estimate post-detection bypass mortality and provide valid estimates of smolt survival in the river reaches. The MSR model provides a robust alternative to the traditional SR model (Dauble et al. 1993).

The modification to the design for the SR model consists of concurrent releases of PIT-tagged fish in the bypass system just downstream from the PIT-tag detector and control fish in the zone of the tailrace where detected and nondetected fish remix. The MSR model explicitly estimates mortality between the detector and the remixing zone at Lower Granite and Little Goose Dams, and adjusts the reach survival estimates ($\hat{S}_1$ and $\hat{S}_2$).

Additional terms for the MSR model (Fig. 2) are defined as follows:

R_{B2} is the number of fish released in the bypass system at Lower Granite Dam; C_{B2} is the number of fish released in the tailrace at Lower Granite Dam; R_{B3} is the number of fish released in the bypass system at Little Goose Dam; C_{B3} is the number of fish released in the tailrace at Little Goose Dam; n_{R2} is the number of fish recovered downstream from the treatment release (R_{B2}); n_{C2} is the number of fish recovered downstream from the control release (C_{B2}); n_{R3} is the number of fish recovered downstream from the treatment release (R_{B3}); n_{C3} is the number of fish recovered downstream from the control release (C_{B3}); τ_2 is the survival probability between detector and remixing zone at Lower Granite Dam; τ_3 is the survival probability between detector and remixing zone at Little Goose Dam; λ_2 is the joint probability of secondary release fish from Lower Granite Dam surviving and being detected downriver; and λ_3 is the joint probability of secondary release fish from Little Goose Dam surviving and being detected downriver.

The likelihood model for the MSR design can be written as the joint likelihood for the primary and secondary releases:

$$
\begin{aligned}
(10)\quad & L(\underset{\sim}{S},\underset{\sim}{p},\underset{\sim}{\tau},\underset{\sim}{\lambda}|\underset{\sim}{R_p},\underset{\sim}{R_B},\underset{\sim}{C_B},\underset{\sim}{m},\underset{\sim}{n}) = \\
& \binom{R_1}{m_{12},m_{13},m_{14}}(S_1p_2)^{m_{12}}(S_1(1-p_2)S_2p_3)^{m_{13}} \\
& \times (S_1(1-p_2)S_2(1-p_3)\lambda)^{m_{14}} \\
& \times (1-S_1(p_2+(1-p_2)S_2p_3+(1-p_2)S_2(1-p_3)\lambda))^{R_1-r_1} \\
& \times \binom{R_2}{m_{23},m_{24}}(\tau_2S_2p_3)^{m_{23}}(\tau_2S_2(1-p_3)\lambda)^{m_{24}} \\
& \times (1-\tau_2S_2(p_3+(1-p_3)\lambda))^{R_2-r_2}\binom{R_3}{m_{34}}(\tau_3\lambda)^{m_{34}}(1-\tau_3\lambda)^{R_3-m_{34}} \\
& \times \binom{R_{B2}}{n_{R2}}(\tau_2\lambda_2)^{n_{R2}}(1-\tau_2\lambda_2)^{R_{B2}-n_{R2}}\binom{C_{B2}}{n_{C2}}(\lambda_2)^{n_{C2}}(1-\lambda_2)^{C_{B2}-n_{C2}} \\
& \times \binom{R_{B3}}{n_{R3}}(\tau_3\lambda_3)^{n_{R3}}(1-\tau_3\lambda_3)^{R_{B3}-n_{R3}}\binom{C_{B2}}{n_{C2}}(\lambda_3)^{n_{C3}}(1-\lambda_3)^{C_{B3}-n_{C3}}
\end{aligned}
$$

Iterative numerical methods were used to estimate reach survival and post-detection bypass survival simultaneously. However, the following formula (the "relative-recovery" estimate) can be given for estimates of post-detection bypass survival:

$$(11)\quad \hat{\tau}_i = \frac{(n_{Ri}/R_{Bi})}{(n_{Ci}/C_{Bi})},\quad \text{for } i = 2 \text{ and } 3.$$

The null hypotheses H_0: $\tau_2 = 1$ and H_0: $\tau_3 = 1$ were tested using likelihood ratio tests (LRT). Fish from the secondary releases were pooled in performing the LRTs.

A critical assumption of the MSR likelihood model (eq. 10) model is that the treatment fish of the paired release have the same survival and capture probabilities as the control fish downstream from the remixing zone (i.e., the difference between the downstream detection rates for the two groups is entirely due to mortality in the bypass system). For paired groups that pass two or more detection and diversion sites, an alternative formulation of the MSR model is available, based on survival probabilities from the point of release to the next site downstream. Post-detection bypass survival probability is then based on relative survival for the two groups, rather than on relative recovery rates.

Results

Assessment of the validity of using PIT-tag data in single release–recapture analysis was first evaluated using Monte Carlo methods to identify nonrobust properties of the model and then by empirical results from replicated field trials.

Monte Carlo simulations

Effect of heterogeneity of individuals on estimates of survival probabilities

Under conditions of heterogeneity of survival probabilities among individuals (violation V7a), the estimates of survival were unbiased, while theoretical variance estimates were slightly inflated (Table 4). Consequently, nominal 95% confidence intervals (eq. 9) covered the true survival probability (S_1 and S_2) slightly more than 95% of the time. These results are consistent with properties of independent but nonidentical Bernoulli trials used to estimate binomial proportions (Feller 1968, pp. 230–231).

Effect of route-specific dam passage mortality on estimates of survival probabilities

When bypass mortality occurred before detection (violation

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Table 4. Results from 1000 Monte Carlo simulations for scenarios with heterogeneous survival rates due to individual differences (violation V7a).

Scenario	Reach	True $\overline{S}_k$	$\overline{\hat{S}}_k$	$\overline{\widehat{\mathrm{Var}}(\hat{S}_k \mid S_k)}$	$s^2_{\hat{S}_k}$	95% CI coverage
V7a.1	Rel–LGR	0.878	0.878	0.000 564	0.000 563	95.0
	LGR–LGO	0.878	0.880	0.001 651	0.001 565	95.4
V7a.2	Rel–LGR	0.598	0.598	0.000 679	0.000 663	94.9
	LGR–LGO	0.898	0.904	0.005 343	0.005 100	95.7

Note: True mean survival probability ($\overline{S}_k$), average survival estimate ($\overline{\hat{S}}_k$), average variance estimate ($\overline{\widehat{\mathrm{Var}}(\hat{S}_k \mid S_k)}$), empirical variance among survival estimates ($s^2_{\hat{S}_k}$), and 95% confidence interval coverage are given. Survival probabilities were estimated for release to Lower Granite Dam (Rel–LGR) and Lower Granite to Little Goose Dam (LGR–LGO) reaches.

V7b) and the dead fish went undetected, there was no bias in overall reach survival estimates ($\overline{\hat{S}}$) or associated variance estimates ($\overline{\widehat{\mathrm{Var}}(\hat{S}_k \mid S_k)}$) (Table 5). Confidence interval coverage for $\hat{S}$ was nominal.

When mortality occurred in the bypass system after detection but before remixing with nondetected survivors, the PIT-tagged fish are counted as survivors. This type of route-specific mortality (violation 8) resulted in biased point estimates and variance estimates of survival and poor confidence interval coverage (Table 5). These simulation results motivated the development of the MSR model and the paired post-detection bypass releases in 1993.

Field trials

Effect of upstream detection on the probability of downstream detection

Daily distributions of detections at Little Goose Dam for the two subgroups of each primary release that passed Lower Granite Dam (i.e., detected or not detected) differed significantly ($P = 0.007$) only for the fifth release. Among the detection distributions at Lower Monumental Dam for four subgroups of each primary release defined by capture histories at Lower Granite and Little Goose Dams, again only the fifth release had significant differences ($P = 0.004$).

Differences in detection distributions at Little Goose Dam may have been the result of a 1- or 2-day delay for fish detected at Lower Granite Dam. However, river conditions over the peak days of passage for both groups were sufficiently stable and unlikely to cause a significant difference in survival or detection probability at Little Goose Dam. Furthermore, the test of homogeneity (TEST 3) proposed by Burnham et al. (1987) did not indicate significantly different survival and capture probabilities for detected and nondetected fish at Lower Granite Dam. The distribution of capture histories at Lower Monumental and McNary Dams did not depend on the capture history at Lower Granite and Little Goose dams for any of the seven primary releases.

Effect of upstream detection on the probability of downstream survival

Estimates (eq. 11) of post-detection bypass survival using relative recovery numbers from paired releases at Lower Granite Dam (τ_2) ranged from 0.915 to 0.986 with a weighted average (weights inversely proportional to respective estimated variances) of 0.950 ± 0.022 (mean ± SE). Based on the weighted average, an approximate 95% confidence interval for post-detection bypass survival at Lower Granite Dam of 0.907–0.993 does not include 1.0, suggesting that significant mortality may have occurred. Likelihood ratio tests based on the model in eq. 10 also indicated significant mortality at Lower Granite Dam ($\chi^2_1 = 4.774$, $P = 0.029$). However, there is some indication that the assumption of equal detection probabilities for the paired releases was violated at Little Goose Dam for the second paired release. Applying the SR model independently to the two groups, the estimated detection probabilities were 0.405 ± 0.028 and 0.502 ± 0.026 for the second treatment and control groups, respectively. The weighted average of post-detection bypass survival at Lower Granite Dam based on the relative survival method was 1.001 ± 0.070. Consequently, conclusions regarding post-detection bypass mortality depend on whether the relative recovery or the relative survival method is used in the analysis of the paired releases. Differential detection probabilities within the paired releases suggest the better estimate of post-detection bypass mortality is provided by the relative survival method. Therefore, survival estimates for the primary releases were calculated using both the SR and MSR models.

Accuracy of model-based estimates of measurement error

For the seven survival estimates in the reach from release to Lower Granite Dam (Table 6), the average estimated sampling variance was 0.000 49 (SD = 0.022 1), while the empirical variance among the seven point estimates of survival was 0.000 12 (SD = 0.010 9). The two variance estimates are of the same order of magnitude, and the model-based variance is greater than the empirical variance. For survival estimates in the Lower Granite Dam to Little Goose Dam reach (Table 7), the average estimate of sampling variance was 0.000 13 (SD = 0.011 4), while the empirical variance among the seven point estimates was 0.000 12 (SD = 0.010 7), almost identical. There was no evidence that the model failed to adequately measure any significant source of variability.

Survival estimates for Snake River reaches

The primary releases, besides testing model assumptions, also provide an opportunity to examine survival of run-of-the-river hatchery-reared yearling chinook salmon during their outmigration to the ocean. However, when examining the resulting survival estimates, it must be remembered that these estimates represent only 1 week in the seasonal and interseasonal history of the river.

The following reach survival estimates are based on the SR model (i.e., assumption of 0% post-detection bypass

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Table 5. Results from 1000 Monte Carlo simulations for scenarios with passage route-specific mortality.

Scenario	Reach	True $\overline{S}_k$	$\overline{\hat{S}}_k$	$\overline{\widehat{\mathrm{var}}(\hat{S}_k \mid S_k)}$	$s^2_{\hat{S}_k}$	95% CI coverage
V7b.1	Rel–LGR	0.855	0.858	0.001 71	0.001 62	95.9
	LGR–LGO	0.855	0.860	0.005 27	0.005 26	95.3
V8.1	Rel–LGR	0.889	0.954	0.002 20	0.002 16	75.3
	LGR–LGO	0.893	0.862	0.005 67	0.005 60	90.3
V7b.2	Rel–LGR	0.855	0.868	0.012 85	0.013 70	95.9
	LGR–LGO	0.855	0.888	0.043 06	0.043 17	94.2
V8.2	Rel–LGR	0.872	0.972	0.018 00	0.017 57	97.0
	LGR–LGO	0.874	0.883	0.048 58	0.052 37	91.4
V7b.3	Rel–LGR	0.875	0.878	0.001 59	0.001 69	94.9
	LGR–LGO	0.880	0.883	0.004 92	0.005 10	95.0
V8.3	Rel–LGR	0.882	0.897	0.001 67	0.001 68	95.2
	LGR–LGO	0.887	0.881	0.004 98	0.004 91	94.2
V7b.4	Rel–LGR	0.894	0.904	0.011 84	0.012 77	94.3
	LGR–LGO	0.898	0.922	0.037 79	0.034 58	94.3
V8.4	Rel–LGR	0.902	0.940	0.013 16	0.013 79	95.8
	LGR–LGO	0.904	0.913	0.037 58	0.035 57	93.2
V7b.5	Rel–LGR	0.448	0.456	0.003 71	0.003 32	95.7
	LGR–LGO	0.456	0.484	0.017 87	0.015 83	94.6
V8.5	Rel–LGR	0.619	1.044	0.022 92	0.022 91	2.3
	LGR–LGO	0.646	0.538	0.023 63	0.022 38	72.1
V7b.6	Rel–LGR	0.604	0.624	0.021 18	0.020 30	93.2
	LGR–LGO	0.608	0.696	0.132 30	0.100 98	92.5
V8.6	Rel–LGR	0.690	1.371	0.214 11	0.198 25	92.4
	LGR–LGO	0.703	0.774	0.472 80	0.287 62	87.3

Note: True survival probability ($\overline{S}_k$), average survival estimate ($\overline{\hat{S}}_k$), average variance estimate ($\overline{\widehat{\mathrm{var}}(\hat{S}_k \mid S_k)}$), empirical variance among survival estimates ($s^2_{\hat{S}_k}$), and 95% confidence interval coverage are given. Survival probabilities were estimated for release to Lower Granite Dam (Rel–LGR) and Lower Granite to Little Goose Dam (LGR–LGO) reaches. Mortality in the bypass system occurs either before detection (violation V7b) or after detection (violation V8) at Lower Granite and Little Goose dams.

mortality). For the river section between Nisqually John and the tailrace of Lower Granite Dam (Table 6), smolt survival estimates ($\hat{S}_1$) ranged between 0.886 ± 0.020 and 0.920 ± 0.024 with a weighted average ($\overline{\hat{S}}_2$) of 0.902 ± 0.004. The $\hat{S}_2$ values between the tailrace of Lower Granite Dam and the tailrace of Little Goose Dam (Table 7) ranged from 0.818 ± 0.034 to 0.902 ± 0.044 with a $\overline{\hat{S}}_2$ of 0.859 ± 0.013. These estimates correspond well with other survival estimates of wild and hatchery-released yearling chinook over the wider range of the 1993 outmigration season reported by Iwamoto et al. (1994), and over the 1994 and 1995 seasons reported by Muir et al. (1995, 1996). Under the SR model, the estimated survival from Nisqually John to the tailrace of Little Goose Dam is 0.775 (= 0.902 × 0.859).

Using the relative recovery method, post-detection bypass mortalities at Lower Granite and Little Goose dams are estimated to be 6% and 0%, respectively. If these survival figures are correct, the pooled estimates of survival for the primary releases are 0.875 ± 0.014 from Nisqually John to Lower Granite Dam tailrace and 0.913 ± 0.021 from Lower Granite Dam tailrace to Little Goose Dam tailrace. The effect of post-detection mortality is to lower the estimated survival rate in the subsequent reach. Essentially, the MSR model redistributes this "extra" dam mortality to the proper reach. Under the MSR model, the estimated survival from Nisqually John to the tailrace of Little Goose Dam is 0.799 (= 0.875 × 0.913) compared with 0.775 under the SR model.

Discussion

By establishing the validity of the statistical and field methodology, we have shown that reliable survival estimates can be obtained from release–recapture models of detection data from PIT-tagged migrant juvenile salmonids in the Snake–Columbia River Basin. The ability to obtain reliable survival estimates is a powerful tool for the investigation, mitigation, and recovery of threatened and endangered salmonid stocks.

Our Monte Carlo simulation studies showed that heterogeneity of survival and detection probabilities among animals had no effects on estimates of mean survival probabilities but resulted in overestimation of the sampling variance and produced confidence intervals that were too wide. Conversely, the fates of fish within a release group are not independent; model-based variance estimates will tend to underestimate the true variance. While it is intuitive that there is heterogeneity among animals, there is no empirical evidence that fates of fish within a group are not independent. The empirical variance estimates from seven replicate releases estimated very near the model-based error variances estimated from the likelihood model. Hence, not only do the point estimates generated by this pilot study appear to be accurate and robust, but the standard errors of the estimates appear to be reliable measures of the uncertainty of the survival estimates. These results indicate the use of PIT-tags and release–recapture models can provide valid estimates of survival probabilities. Since 1993, diversion

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Table 6. Estimated survival probabilities, estimated sampling variances, and average estimated variance from release to Lower Granite Dam tailrace based on primary releases.

Release	Point estimate of survival ($\hat{S}_{1i}$)	Estimated variance ($\widehat{\text{Var}}(\hat{S}_{1i}\|S_{1i})$)
R_{11}	0.920	0.000 576
R_{12}	0.900	0.000 361
R_{13}	0.911	0.000 484
R_{14}	0.903	0.000 529
R_{15}	0.901	0.000 484
R_{16}	0.895	0.000 576
R_{17}	0.886	0.000 400
Overall estimated variance		0.000 487 (0.022 1)
Empirical variance ($s^2_{\hat{S}_{1i}}$)		0.000 119 (0.010 9)

Note: Values for average estimated variance and empirical variance are variance and standard deviation.

Table 7. Estimated survival probabilities, estimated sampling variances, and average estimated variance from Lower Granite Dam tailrace to Little Goose Dam tailrace based on primary releases.

Release	Point estimate of survival ($\hat{S}_{2i}$)	Estimated variance ($\widehat{\text{Var}}(\hat{S}_{2i}\|S_{2i})$)
R_{11}	0.888	0.001 52
R_{12}	0.889	0.000 84
R_{13}	0.831	0.000 96
R_{14}	0.818	0.001 16
R_{15}	0.831	0.001 37
R_{16}	0.902	0.001 94
R_{17}	0.869	0.001 30
Overall estimated variance		0.000 130 (0.011 4)
Empirical variance ($s^2_{\hat{S}_{2i}}$)		0.000 115 (0.010 7)

Note: Values for average estimated variance and empirical variance are variance and standard deviation.

systems have been completed at Lower Monumental and McNary dams extending the capability to perform survival studies much further downriver.

The assumption that survival and detection probabilities were not affected by upstream capture histories was evaluated by comparing temporal passage distributions for detected and nondetected smolts. Coincident downstream migrations were evident in six of seven cases. In one case, the timing was delayed 1 or 2 days for detected fish. Coincident passage is a sufficient condition for assuring that all fish are exposed to similar survival and detection conditions. However, coincident passage is not necessary for equal probabilities if river conditions vary little over a 1- or 2-day period. Indeed, for the group with apparent noncoincident passage, the Burnham et al. (1987) test of homogeneity (TEST 3) found no significant difference in downstream capture histories for groups of fish with differing upstream detection histories.

Our smallest release group of only 797 PIT-tagged fish on 20 April 1993 resulted in standard errors of 0.024 and 0.044 on survival estimates from the release to Lower Granite Dam and Lower Granite Dam to Little Goose Dam reaches, respectively. The largest release of 1405 fish resulted in standard errors of 0.020 and 0.036 for the two reaches, respectively. These levels of precision for survival estimates have not been attainable using more conventional marking techniques in the past (e.g., freeze-brand, fin-clipping), even with tens of thousands of marked fish. Hence, the PIT-tag has the capability of providing accurate and precise estimates of survival using a minimum number of fish at a time when the need for information is the greatest and the opportunity to handle large numbers of fish is low because of listings of salmonids stocks under the Endangered Species Act.

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References

Burnham, K.P., Anderson, D.R., White, G.C., Brownie, C., and Pollock, K.H. 1987. Design and analysis methods for fish survival experiments based on release–recapture. Am. Fish. Soc. Monogr. No. 5.

Cormack, R.M. 1964. Estimates of survival from the sighting of marked animals. Biometrika, **51**: 429–438.

Dauble, D.D., Skalski, J.R., Hoffmann, A., and Giorgi, A.E. 1993. Evaluation and application of statistical methods for estimating smolt survival. Report to the Bonneville Power Administration. Contract No. DE-AC06-76RL0 1830. (Available from Bonneville Power Administration - PJ, P.O. Box 3621, Portland, OR 97208, U.S.A.)

Durkin, J.T., and Park, D.L. 1967. Purse seine for sampling juvenile salmon. Prog. Fish Cult. **29**: 56–59.

Feller, W. 1968. An introduction to probability theory and its applications. Vol. 1. Wiley & Sons, New York.

Hudson, D.J. 1971. Interval estimation from the likelihood function. J. R. Stat. Soc. B, **33**: 256–262.

Iwamoto, R.N., Muir, W.D., Sandford, B.P, McIntyre, K.W., Frost, D.A., Williams, J.G., Smith, S.G., and Skalski, J.R. 1994. Survival estimates for the passage of juvenile chinook salmon through Snake River dams and reservoirs. Annual Report 1993. Bonneville Power Administration, Portland, Oreg.

Jolly, G.M. 1965. Explicit estimates from capture–recapture data with both death and immigration—stochastic model. Biometrika, **52**: 225–247.

Muir, W.D., Smith, S.G., Iwamoto, R.N., Kamikawa, D.J., McIntyre, K.W., Hockersmith, E.E., Sandford, B.P., Ocker, P.A., Ruehle, T.E., Williams, J.G., and Skalski, J.R. 1995. Survival estimates for the passage of juvenile chinook salmon through Snake River dams and reservoirs. Annual Report 1994. Bonneville Power Administration, Portland, Oreg.

Nielsen, L.A. 1992. Methods of marking fish and shellfish. Am. Fish. Soc. Spec. Publ. No. 23(5). pp. 104–109.

Prentice, E.F. 1990. A new telemetry tag for fish and crustaceans. NOAA Tech. Rep. NMFS No. 85. pp. 1–9.

Prentice, E F., Flagg, T.A., and McCutcheon, C S. 1987. A study to determine the biological feasibility of a new fish tagging system, 1986–1987. Bonneville Power Administration, Portland, Oreg.

Prentice, E.F., Flagg, T.A., and McCutcheon, C.S. 1990*a*. Feasibility of using implantable passive integrated transponder (PIT) tags in salmonids. Am. Fish. Soc. Symp. **7**: 317–322.

Prentice, E.F., Flagg, T.A., McCutcheon, C.S., and Brastow, D. 1990*b*. PIT-tag monitoring systems for hydroelectric dams and fish hatcheries. Am. Fish. Soc. Symp. **7**: 323–334.

Prentice, E.F., Flagg, T.A., McCutcheon, C.S., Brastow, D., and

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Cross, D. 1990c. Equipment, methods, and an automated data-entry station for PIT tagging. Am. Fish. Soc. Symp. **7**: 335–340.

Seber, G.A.F. 1965. A note on the multiple recapture census. Biometrika, **52**: 249–259.

Sims, C.W., and Ossiander, F.J. 1981. Migrations of juvenile chinook salmon and steelhead trout in the Snake River from 1973–1979. A research summary. National Marine Fisheries Service, Seattle, Wash.

Skalski, J.R., Hoffmann, A., and Smith, S.G. 1993. Testing the significance of individual and cohort-level covariates in animal survival studies. *In* The use of marked individuals in the study of bird population dynamics: models, methods, and software. *Edited by* J.D. Lebreton and P.M. North. Birkhauser Verlag, Basel, Switzerland. pp. 1–17

Smith, S.G., Skalski, J.R., Schlechte, W., Hoffmann, A., and Cassen, V. 1994. SURPH.1 manual: statistical survival analysis for fish and wildlife tagging studies. Bonneville Power Administration, Portland, Oreg.

Snedecor, G.W., and Cochran, W.G. 1989. Statistical methods. Iowa State University Press, Ames.

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Natural isotope indicators of fish migration at Prudhoe Bay, Alaska

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Abstract: A dichotomy in the natural stable carbon isotope abundance measured in tissues of obligate freshwater and marine fishes from the Alaskan Arctic coastal plain suggested that the methodology can be used to differentiate recent freshwater from marine feeding in migratory fishes. Natural stable carbon isotope ratio of migratory fishes reflected differences of feeding habitat in relation to known life-history patterns. Use of the stable isotope methodology as a tool for proxy analysis of fish behavior in present and future Arctic environmental monitoring studies is suggested from analysis of age-specific isotopic ratio differences in broad whitefish (*Coregonus nasus*) and Arctic cisco (*Coregonus autumnalis*).

Résumé : Une dichotomie dans l'abondance des isotopes stables naturels de carbone mesurée dans les tissus de poissons strictement marins et dulcicoles de la plaine côtière de l'Arctique, en Alaska, laisse supposer que la méthode peut être utilisée pour distinguer, chez les espèces migratrices, l'alimentation récente en eau douce de l'alimentation en mer. La rapport des isotopes stables naturels de carbone chez les poissons migrateurs reflète des différences dans l'habitat d'alimentation qui sont en rapport avec des étapes connues du cycle vital. L'analyse des différences des rapports isotopiques selon l'âge chez le corégone tschir (*Coregonus nasus*) et le cisco arctique (*Coregonus autumnalis*) indique que la méthode des isotopes stables peut être utilisée comme outil pour l'analyse substitutive du comportement du poisson dans des études courantes et futures de surveillance de l'environnement arctique
[Traduit par la Rédaction]

Introduction

Isotope chemistry is a powerful tool for use in ecological studies because of naturally existing isotope gradients and the fidelity of consumer isotope ratios with their diet (Fry and Sherr 1984; Owens 1987; Wada et al. 1991). Large gradients occur in the natural abundance of the stable heavy isotope of carbon, ^{13}C, as well as the radioactive isotope of carbon, ^{14}C, between freshwater and marine habitats of the Alaskan Arctic coastal plain because of the existence of massive ^{14}C-depleted (because of radioactive decay) and ^{13}C-depleted (Barnett 1994) peat deposits. Peat provides an important carbon source (directly via peat-consuming invertebrates and indirectly via respiration of peat carbon) to coastal plain freshwater food chains (including anadromous and (or) amphidromous fishes) but not to coastal marine food chains (Schell 1983; Schell and Zieman 1989). Because stable isotope ratios are conserved during feeding processes, they make effective tracers of food sources used by anadromous and amphidromous fishes, enabling one to distinguish between peat versus marine carbon utilization by fishes (and other consumers).

The data obtained from stable isotope measurements are unique in that they trace assimilated material. Nitrogen stable isotope ratios provide excellent definition of relative trophic level (Fry 1988; Wada et al. 1991; Hobson and Welch 1992; Kiriluk et al. 1995). The heavy isotope of nitrogen, ^{15}N, is enriched by about 0.34% (or 3.4‰ in conventional delta units, see Materials and methods) with each trophic level (Minagawa and Wada 1984) and can accurately indicate the trophic level of species within an ecosystem (Kling et al. 1992; Cabana and Rasmussen 1994). Carbon isotope signatures were used to trace multiple sources of carbon into food webs (Fry and Sherr 1984; Wada et al. 1991) by exploiting the ^{13}C gradient in Alaskan Arctic coastal plain food web carbon sources (Schell 1983; Schell and Zieman 1989) while using carbon to nitrogen (C/N) ratio and nitrogen stable isotope measurements to correct $^{13}C/^{12}C$ values for lipid storage and trophic level isotope effects (Kline 1997).

Fishes of the genus *Coregonus* and *Salvelinus* are abundant in the coastal and freshwaters of the Alaskan Arctic. In addition to being obligate freshwater spawners, they undergo summer feeding migrations into coastal waters during which they take on lipid reserves to maintain body condition through the subsequent winter season (Craig 1989; Fechhelm et al. 1995, 1996). Nearshore Beaufort Sea monitoring programs focusing on subsistence-harvested and commercially harvested Arctic cisco (*Coregonus autumnalis*), least cisco (*Coregonus sardinella*), and broad whitefish (*Coregonus nasus*) have been ongoing since the 1970s because of concerns over potential impacts on these species from oil development (Gallaway et al. 1991). Much of the focus of these monitoring studies has been assessing the impact of causeways because of their potential for altering the migratory behavior of these species (Gallaway et al. 1991).

These coregonine species are either amphidromous, because they seasonally migrate between the freshwater and marine environments and overwinter in freshwater, or anadromous,

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because they undertake similar seasonal migrations but overwinter in brackish river delta environments (Craig 1984, 1989). Arctic cisco are anadromous, and they eventually spawn in freshwater tributaries of the Mackenzie River, at ages 6–9 (Gallaway et al. 1983). Least cisco, broad whitefish, and Dolly Varden (*Salvelinus malma*, Salmoninae) are amphidromous because they overwinter in freshwater. All of these species seasonally migrate out of river systems (deltas for Arctic cisco) into the nearshore Beaufort Sea to forage along the coast, returning in the fall to the rivers or river deltas to overwinter (Craig 1989). Maintenance of these populations depends on their continued ability to move back and forth between the freshwater and marine environments. In some portions of the Alaskan Arctic, the migratory pathways are complex because of the low topology and thermokarst features of the Arctic coastal plain and consequent intricate and tortuous pathways among lakes, streams, lagoons, and open water.

We hypothesized that stable isotope composition of fish tissues could be used to discern feeding strategies of the different life-history forms of Arctic fishes. Fish feed either on marine-derived or freshwater-derived production, depending on their life-history form or stage (freshwater resident, marine resident, or anadromous and (or) amphidromous). Each form tends to feed at a specific trophic level because of metabolic requirements, mouth structure, competition, and seasonal food availability. Hypothetically, the $^{13}C/^{12}C$ ratio in fish tissues can be used to indirectly determine migratory behavior by knowing where a fish sample was collected in relation to potential carbon sources. For example, a fish obtained from the marine habitat but containing a carbon signature consistent with freshwater feeding had to have recently migrated there. If a fish "switches" to alternative carbon sources because of environmental pressures (temperature–salinity changes, crowding, etc.), there will be a concomitant change in their isotopic composition.

This study examines $^{15}N/^{14}N$ and $^{13}C/^{12}C$ ratios in tissues of Alaskan North Slope freshwater, anadromous and (or) amphidromous, and marine fishes to explore the possible use of tissue isotope chemistry in Arctic ecological studies. Our objectives were to validate this methodology and to determine carbon signature differences in these different ecological life forms of Arctic fishes.

Materials and methods

Anadromous Arctic cisco and amphidromous least cisco, broad whitefish, and Dolly Varden were collected in fyke nets in coastal waters of the Prudhoe Bay region, Alaska (Fig. 1*a*), during the summers of 1994 and 1995 following the methods of Fechhelm et al. (1995, 1996). Two seasonal samples were collected each year, one in early season (24 June to 23 July 1994 and 23 June to 4 July 1995) and one in late season (11–22 August 1994 and 14–20 August 1995). Subsamples of fish were measured for length to the nearest millimetre. Saggital otoliths were excised and then aged by counting annuli under a dissecting microscope at 10–70× magnification. Marine fourhorn sculpin (*Myoxocephalus quadricornis*) and Arctic flounder (*Pleuronectes glacialis*) were collected during the summer in the coastal fyke nets (above) and from gill nets set near the Chipp River delta (Fig. 1*b*), while the freshwater species Arctic grayling (*Thymallus arcticus*), lake trout (*Salvelinus namaycush*), longnose sucker (*Catostomus catostomus*), burbot (*Lota lota*), ninespine stickleback (*Pungitius pungitius*), and northern pike (*Esox lucius*) were collected from gill and fyke nets placed in Teshekpuk Lake (1992) and in the Chipp River (1994 and 1995).

Whole fish carcasses (from Prudhoe Bay) or epaxial muscle tissue samples (from Teshekpuk Lake and Chipp River) were frozen and sent to our laboratories in either Fairbanks (1994) or Cordova (1995) for preparation for isotopic analysis. Preparation consisted of sampling epaxial muscle from Prudhoe Bay samples, followed by freeze-drying. Epaxial muscle samples sampled in the field (Teshekpuk Lake and Chipp River samples) were freeze-dried directly. Freeze-dried samples were ground to a fine powder with a dental amalgamator (Crescent Dental Wig-L-Bug). Ground freeze-dried samples stored in LSC vials were sent to the Stable Isotope Facility at the University of Alaska Fairbanks where replicate aliquots of ~1.5 mg were weighed to the nearest microgram and loaded into combustion boats for mass spectrometric analysis.

Isotopic determination

A Europa Scientific model 20/20 stable isotope analyzer equipped with a Europa Scientific Roboprep sample preparation and purification unit was used for the analysis. Analytical results include $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios in standard delta units, $\delta^{13}C$ and $\delta^{15}N$, respectively, and percent carbon (%C) and percent nitrogen (%N) (grams carbon or nitrogen per gram dry weight).

The standard delta notation is used to express stable isotope ratios relative to international standards (air for nitrogen and Vienna Peedee belemnite (VPDB) for carbon) and is defined by the following expression:

$$(1) \qquad \delta^{15}N \text{ or } \delta^{13}C = \left(\frac{R_{sample}}{R_{standard}} - 1\right) \times 1000‰$$

where $R = {}^{15}N/{}^{14}N$ or $^{13}C/^{12}C$. The isotope standards have delta values of 0 by definition, i.e., $\delta^{15}N = 0$ for atmospheric N_2. Naturally occurring $\delta^{15}N$ and $\delta^{13}C$ values observed in biota range from ~0 to ~+20 and from ~0 to ~−50, respectively. Negative $\delta^{13}C$ values reflect the relative enrichment of ^{13}C in the limestone standard compared with biota.

Replicate isotopic analyses were performed on each sample using aliquots of ~1.5 mg dry weight. Samples were rerun when replication was poor (difference >0.6‰). Typically, replication yielded results that were within 0.2‰. The %C and %N data were used to calculate C/N atomic ratios. Means of $\delta^{13}C$, $\delta^{15}N$, and C/N replicates were used for data modeling. Although $\delta^{15}N$ values of biota vary principally as a function of trophic level (Fry 1988), there can be significant nitrogen source isotope effects (Kline et al. 1997). Determination that nitrogen source isotope effects were not present was based on comparing $\delta^{15}N$ values of similar trophic level fishes across the study area. Following validation, $\delta^{15}N$ values were then used to normalize for the trophic enrichment of ^{13}C using the procedure described below. The lipid normalization procedure of McConnaughey and McRoy (1979) was used to remove lipid isotope effects (DeNiro and Epstein 1977). The combined normalizations for trophic level and lipid storage resulted in ^{13}C values dependent primarily on source, thus enabling the identification of the source of carbon in samples based on the natural ^{13}C gradient (Kline 1997).

Normalization protocols

Normalization for lipid content is needed because lipid synthesis and storage can alter ^{13}C content (DeNiro and Epstein 1977). The normalization technique used was developed by McConnaughey and McRoy (1979) and validated by Kline (1997). The C/N atomic ratio derived from mass spectrometry provided an inexpensive proxy for lipid content that was used to calculate lipid-normalized $\delta^{13}C$ (expressed as $\delta^{13}C'$).

The consistant enrichment of ^{15}N in animal tissues compared with that in their diet was used to compute a relative trophic level (TL) by comparing $\delta^{15}N$ values with a reference TL value (e.g., Cabana and Rasmussen 1994). The $\delta^{15}N$ values of higher TLs were calculated by

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Fig. 1. (*a*) Fish and hydrographic monitoring stations (diamonds) in the Prudhoe Bay region (1994 and 1995) and (*b*) freshwater (circles) and marine (square) fish sampling stations in the Ikpikpuk River region including Teshekpuk Lake (1992) and Chipp River (1994 and 1995).

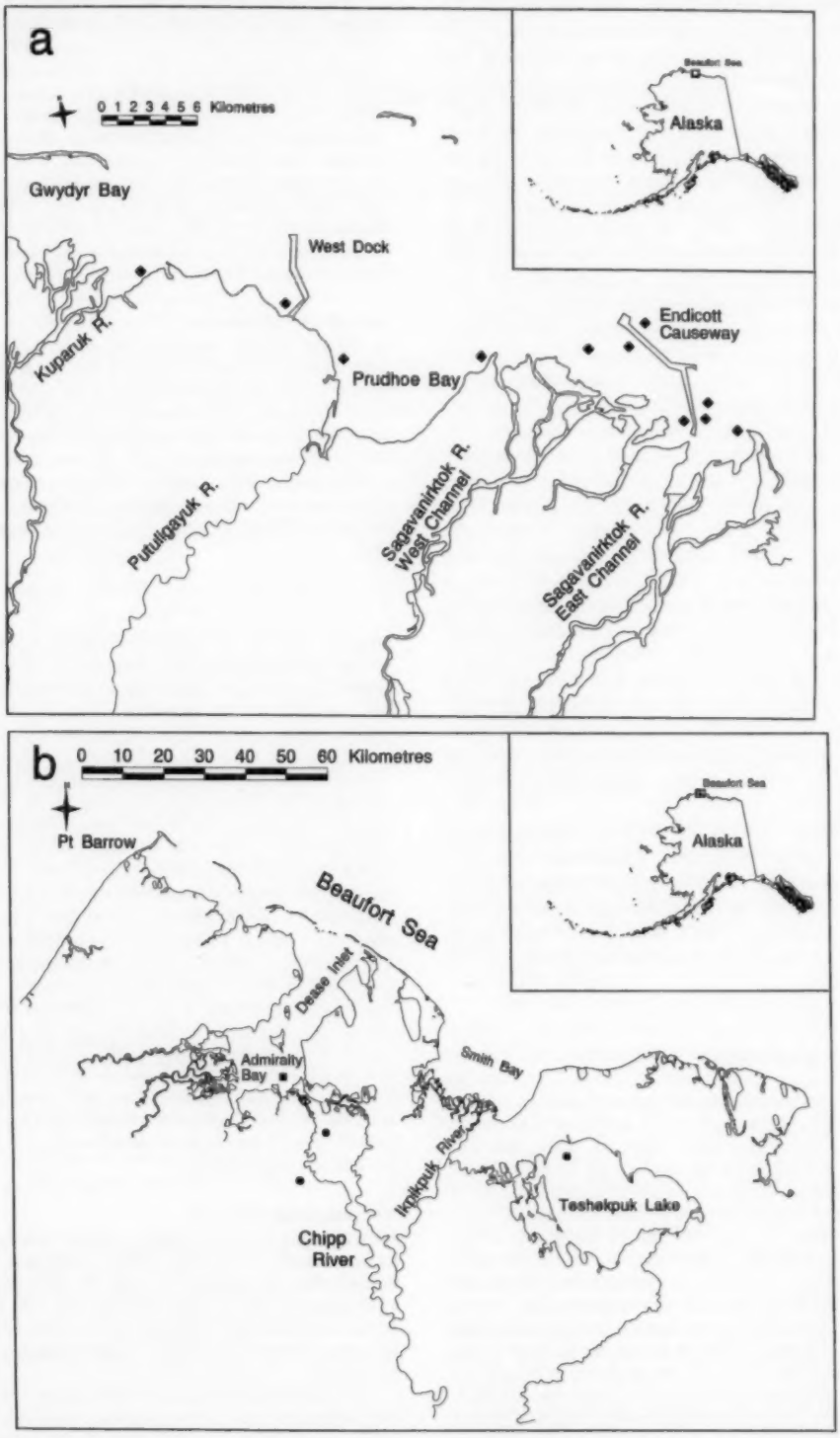

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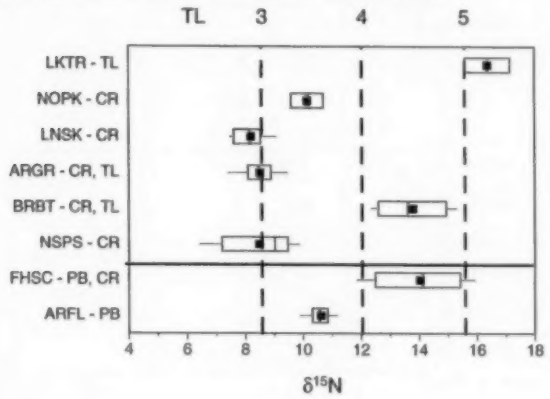
Fig. 2. Determination of TL (upper axis label) from $\delta^{15}N$ with variability indicated by computer-fitted (Deltagraph Pro 3.0, Deltapoint Inc.) box and whisker plots. Freshwater-resident fishes (LKTR, lake trout ($N = 2$); NOPK, northern pike ($N = 2$); LNSK, longnose sucker ($N = 16$); ARGR, Arctic grayling ($N = 22$); BRBT, burbot ($N = 12$); NSPS, ninespine stickleback ($N = 25$)) were collected from the Alaskan Arctic coastal plain in 1992 and 1994, while marine fishes (FHSC, fourhorn sculpin ($N = 22$); ARFL, Arctic flounder ($N = 19$)) were collected from the Alaskan Arctic coastal plain in 1994. TL, CR, and PB after species codes refer to the sampling locations Teshekpuk Lake, Chipp River, and Prudhoe Bay, respectively. The whiskers indicate the 10th and 90th percentiles. The 25th, 50th, and 75th percentiles are indicated by the boxes whereas the mean value is shown as a symbol.



adding the trophic enrichment factor, ϵ_N (see eq. 2 below), to a reference TL value. Although obligate herbivores, i.e., TL = 2, thus well defined by TL, are suitable for the reference TL, a substantial sample size (e.g., ~1000) may be required (Kline 1997). Instead, TLs of fishes in this study were determined in relation to low-TL fishes which were assumed to be TL = 3.

Normalization for TL enabled comparison of $\delta^{13}C'$ values among species or individuals within a species with multiple TL, since residual $^{13}C/^{12}C$ delta values reflected carbon source. The normalization procedure used the trophic enrichment factors, ϵ_C and ϵ_N (Fry and Sherr 1984; Minagawa and Wada 1984), and the $\delta^{15}N$ value of the reference TL. Normalized values were computed using the following relationship:

$$(2) \quad \delta^{13}C'_{TL} = \delta^{13}C' - \epsilon_C/\epsilon_N(\delta^{15}N_{sample} - \delta^{15}N_{reference})$$

where $\delta^{13}C'_{TL}$ is the ^{15}N-based TL-normalized derivative of $\delta^{13}C'$, $\epsilon_C = 1$, and $\epsilon_N = 3.4$.

Validation of trophic level determination and normalization procedures

In general, $\delta^{15}N$ of aquatic organisms reflect their TL (Owens 1987; Fry 1988; Wada et al. 1991; Cabana and Rasmussen 1994). Although $\delta^{15}N$ values of terrestrial, freshwater, and estuarine organisms are similar (Owens 1987), processes that introduce nitrogen with anomalous $\delta^{15}N$ values (thus affecting TL assessment) to the system may occur (e.g., Kline et al. 1997), particularly at the freshwater–marine ecotone (France 1995). Validation consisted of demonstrating no nitrogen source isotope effect in nonmigratory fish species from the North Slope. Their $\delta^{15}N$ variability was qualitatively assessed in relation to known feeding habits (Craig and McCart 1976; Craig et al. 1984; Craig 1989). The lack of significant nitrogen source isotope effect would be confirmed if the variability in $\delta^{15}N$ accounted for by TL was greater than differences in $\delta^{15}N$ among species of similar TL.

Mixing model

The following isotopic mixing model based on Kline et al. (1997) was used to assess the percentage of a source of a given element in a consumer, given the existence of two sources with a significant stable isotope disparity:

$$(3) \quad \%A = \frac{\delta_B - \delta_{sample}}{\delta_B - \delta_A} \times 100\%$$

where δ_A and δ_B are the delta values of the two sources and δ_{sample} is the delta value of the sample.

Results

Freshwater and marine fishes

Nonmigratory fishes, consisting of freshwater species from the Chipp River and Teshekpuk Lake and marine species from the Prudhoe Bay region and the mouth of the Chipp River, had $\delta^{15}N$ ranging from ~7 to ~17 (Fig. 2). The most positive $\delta^{15}N$ values, ~17, were found in Teshekpuk Lake lake trout. Longnose sucker, Arctic grayling, and ninespine stickleback had $\delta^{15}N$ ~8.5, which was assumed to correspond to TL = 3. Higher TLs were estimated in relation to TL = 3 (Fig. 2). Northern pike, Arctic flounder, burbot, and fourhorn sculpin had $\delta^{15}N$ values >8.5, corresponding to TL >3, but less than the $\delta^{15}N$, and therefore TL, of lake trout.

Nonmigratory fishes were dichotomous in $\delta^{13}C'_{TL}$ with marine species' values greater than freshwater species' values by at least 2‰ (Fig. 3*a*). Within the freshwater group, lake trout and burbot had $\delta^{13}C'$ elevated by ~1‰ compared with the others. Normalization of $\delta^{13}C'$ values for trophic level (i.e., $\delta^{13}C'_{TL}$) removed this difference, making lake trout and burbot more similar to other freshwater fishes (Fig. 3*b*). Only ninespine stickleback had a very broad $\delta^{13}C'$ range. In summary, fishes feeding in freshwater had $\delta^{13}C'_{TL}$ ~–30 to ~–27 whereas fishes feeding in the marine environment had $\delta^{13}C'_{TL}$ ~–22.

Anadromous and (or) amphidromous species

Fishes that migrate between freshwater and marine habitats had $\delta^{13}C'_{TL}$ ranging from –30 to –21, and thus encompassed the range of $\delta^{13}C'_{TL}$ values found for marine and freshwater nonmigratory species (Fig. 4, compare with Fig. 3*b*). Migratory species had distinctive curves when $\delta^{13}C'_{TL}$ and $\delta^{15}N$ were plotted as a function of body size (Figs. 4 and 5). The data suggest shifts in food source (Fig. 4) and TL (Fig. 5) as a function of length (and thus age) as well as differences among the species.

Cohort feeding histories

Shifts in $\delta^{13}C'_{TL}$ and $\delta^{15}N$ values of Arctic cisco and broad whitefish by cohort or year-class (Fig. 6) suggest age-specific differences in food source or TL during 1994–1995. Noteworthy is the shift to more positive $\delta^{13}C'_{TL}$ values in the older age-classes. Interannual variation in $\delta^{13}C'_{TL}$ was apparent even in older fish (ages 4–6, i.e., 1990 and 1991 year-classes).

The relative importance of marine carbon in the feeding history of the broad whitefish and Arctic cisco cohorts shown in Table 1 was determined using as end members δ_A and δ_B (eq. 3), the $\delta^{13}C'_{TL}$ values of obligate marine and freshwater fishes which were ~–22 ± 0.5 and ~–28 ± 1.0, respectively (Fig. 3*b*). The data suggest 100% dependence on marine carbon by age 3 for both species.

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Discussion

Trophic level

Alaska Arctic coastal plain fish $\delta^{15}N$ values and interpreted TLs were similar to those reported in the literature and generally consistent with no $\delta^{15}N$ source effects (France 1995), supporting $\delta^{15}N$ value based TL estimation and normalization of $\delta^{13}C'$ for the study area. The highest $\delta^{15}N$ value of +17, and therefore highest relative TL of 5 determined for lake trout in our study, was similar to the mean $\delta^{15}N$ value and interpreted TL of Lake Ontario lake trout (Kiriluk et al. 1995), although greater than that reported at two sites in the lower Mackenzie River basin, Canada (Hesslein et al. 1991). Conversely, the $\delta^{15}N$ of northern pike found in the Chipp River was less than those from the Kukjuktuk Creek system and a few of those from Travaillant Lake, both in the Mackenzie River system (Hesslein et al. 1991), while ninespine stickleback from all Mackenzie River system and this study's sites were comparable. Longnose sucker from the Chipp River had $\delta^{15}N$ values that were similar to those of white sucker from Travaillant Lake (Hesslein et al. 1991). The $\delta^{15}N$ values of fourhorn sculpin from Prudhoe Bay and the Chipp River were similar to the $\delta^{15}N$ reported for Arctic sculpin (*Myoxocephalus scorpiodes*) from the Canadian high Arctic (Hobson and Welch 1992). Broad whitefish were consistently lower in $\delta^{15}N$ than Arctic cisco, least cisco, or Dolly Varden, implying a lower TL (Fig. 5) which is also anatomically suggested by their small gape and mollusc and aquatic insect feeding habit (McPhail and Lindsey 1970).

$^{13}C/^{12}C$ gradient

The difference in $\delta^{13}C'_{TL}$ values of obligate freshwater and coastal marine fishes (Fig. 3*b*) confirms the existence of a $^{13}C/^{12}C$ gradient in Alaskan Arctic coastal plain biota reported by Schell (1983) and Schell and Zieman (1989). Furthermore, trends in isotopic composition in relation to the size of migratory fishes (Fig. 4) suggest feeding habit shifts dependent on migratory behavior that are consistent with known life-history patterns (Craig 1989). For example, Craig (1989) described two types of life-history patterns of coastal plain anadromous fishes. The char life-history pattern of delayed migration from freshwater involves fry remaining year-round in streams until age 3 or 4 when they begin annual migrations to sea to feed. This life-history pattern is reflected in the Dolly Varden $\delta^{13}C'_{TL}$, since the switch to the more positive $\delta^{13}C'_{TL}$ of marine carbon occurred at a larger size of nearly 300 mm in length (age ~4, Craig 1989). These results contrast with broad whitefish and Arctic cisco which follow the cisco life-history pattern (Craig 1989) where fish annually migrate to the marine environment to feed at all ages. Accordingly, the broad whitefish and Arctic cisco data show the marine $\delta^{13}C'_{TL}$ signature by 100 mm (Fig. 4*b*). The consistency of $\delta^{13}C'_{TL}$ with known life-history patterns of Alaskan Arctic coastal plain fishes suggests that $\delta^{13}C'_{TL}$ can be used as a migratory indicator in this region. This is unlike the Mackenzie River delta area, which does not have a $^{13}C/^{12}C$ gradient (Hesslein et al. 1991).

Age-dependent isotopic variability and shifts

Because of the predictable relationship between natural stable isotope abundance of consumers and their diet (reviewed by Wada et al. 1991), it is being used here to characterize the recent feeding history of Prudhoe Bay area fishes as either freshwater or marine. Juvenile fishes rapidly change their isotopic composition in proportion to addition of new tissue, while differences in isotopic signatures between individuals in groups of older, slow-growing fish reflect different food "choices" because temporal variations are averaged out (Hesslein et al. 1993). The potential diet choice in this study consisted of the spatial and apparent isotopic dichotomy between freshwater and marine carbon (Fig. 3). Arctic fishes are generally long-lived and have slow growth, especially upon reaching sexual maturity (Craig 1989). Based on the results of Hesslein et al. (1993), mature fishes were not expected to vary significantly with time, since temporal variation in feeding would be averaged out. However, the variability in both $\delta^{15}N$ and $\delta^{13}C'_{TL}$ of coregonines in our study did not appear to decrease with increased fish size as expected (Figs. 4 and 5). In contrast, Dolly Varden decreased in isotopic range as a function of size. Larger (>300 mm) Dolly Varden range by about 2‰ in both $\delta^{15}N$ and $\delta^{13}C'_{TL}$, similar to coregonines. However, smaller Dolly Varden exhibited far greater ranges compared with the coregonines, suggesting a greater diversity of feeding niches by individual fish. For example, fish between 250 and 300 mm in length ranged from 100% freshwater feeding to 100% marine feeding and had a two-TL range (Figs. 4 and 5).

Fig. 3. Dichotomy in (*a*) $\delta^{13}C'$ and (*b*) $\delta^{13}C'_{TL}$, shown as box and whisker plots, between two marine and five freshwater fishes as in Fig. 2. Variation in $\delta^{13}C'$ among freshwater species due to differences in TL shown in Fig. 3*a* are removed in Fig. 3*b*.

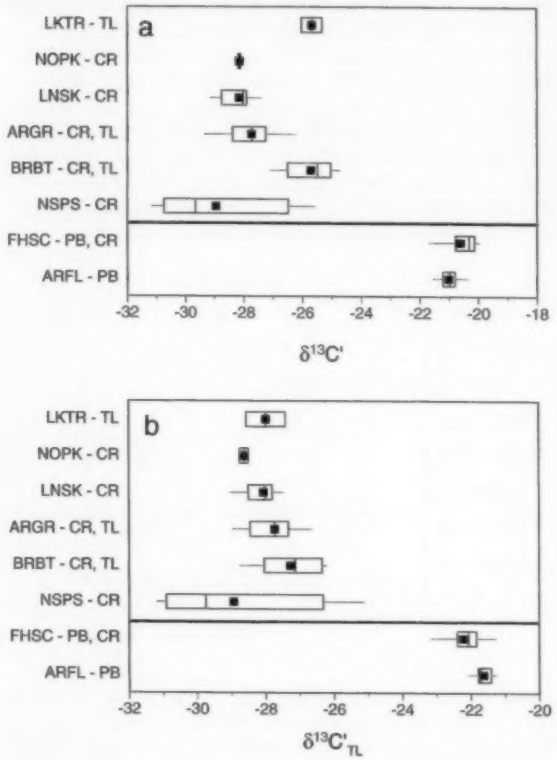

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Fig. 4. $\delta^{13}C'_{TL}$ shifts as a function of length of four North Slope salmonid fishes that are anadromous or amphidromous (Dolly Varden char ($N = 46$) from 1994 (triangles, dotted line), least cisco ($N = 57$) from 1994 (squares, dashed–dotted line), Arctic cisco ($N = 148$) from 1994 and 1995 (crosses, dashed line), and broad whitefish ($N = 181$) from 1994 and 1995 (circles, solid line)) sampled in the Sagavanirktok River delta suggest species-dependent change in carbon source (M, marine; T, transitional; F, freshwater) during life history. Second-order polynomial regressions were computer-fitted (Deltagraph Pro 3.0, Deltapoint Inc.) to the data. The delayed shift in Dolly Varden char is consistent with this species' life-history pattern (Craig 1989).

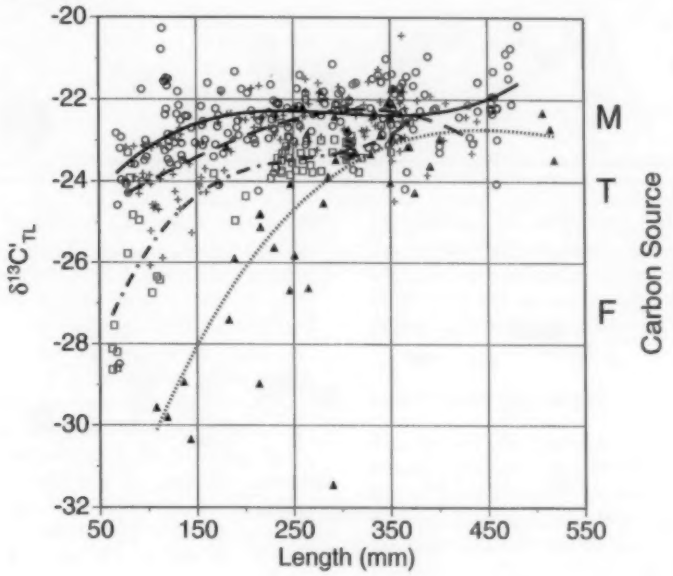

Fig. 5. Shifts in $\delta^{15}N$ as a function of length four North Slope salmonid fishes that are anadromous or amphidromous (Dolly Varden char ($N = 46$) (triangles, solid line), least cisco ($N = 57$) (crosses, dashed line), Arctic cisco ($N = 148$) (circles, dotted line), and broad whitefish ($N = 181$) (squares, dashed–dotted line)) sampled in the Sagavanirktok River delta suggest species-dependent differences in relative TL as well as increases during life history. Regression lines are second-order computer-fitted to the data as in Fig. 4.

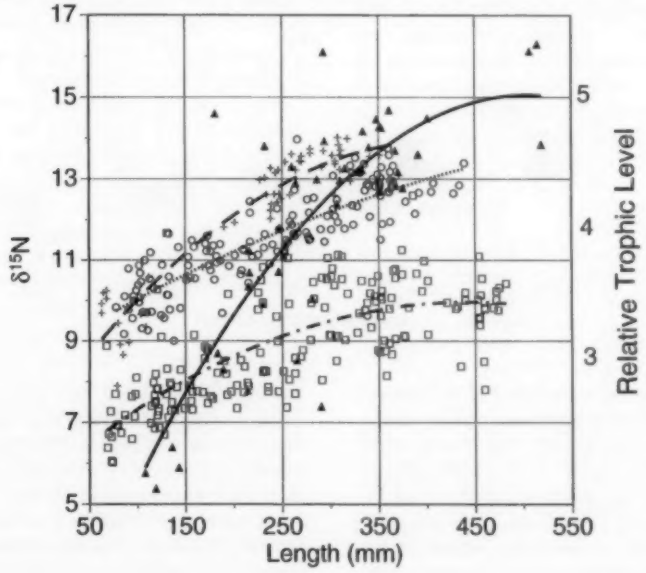

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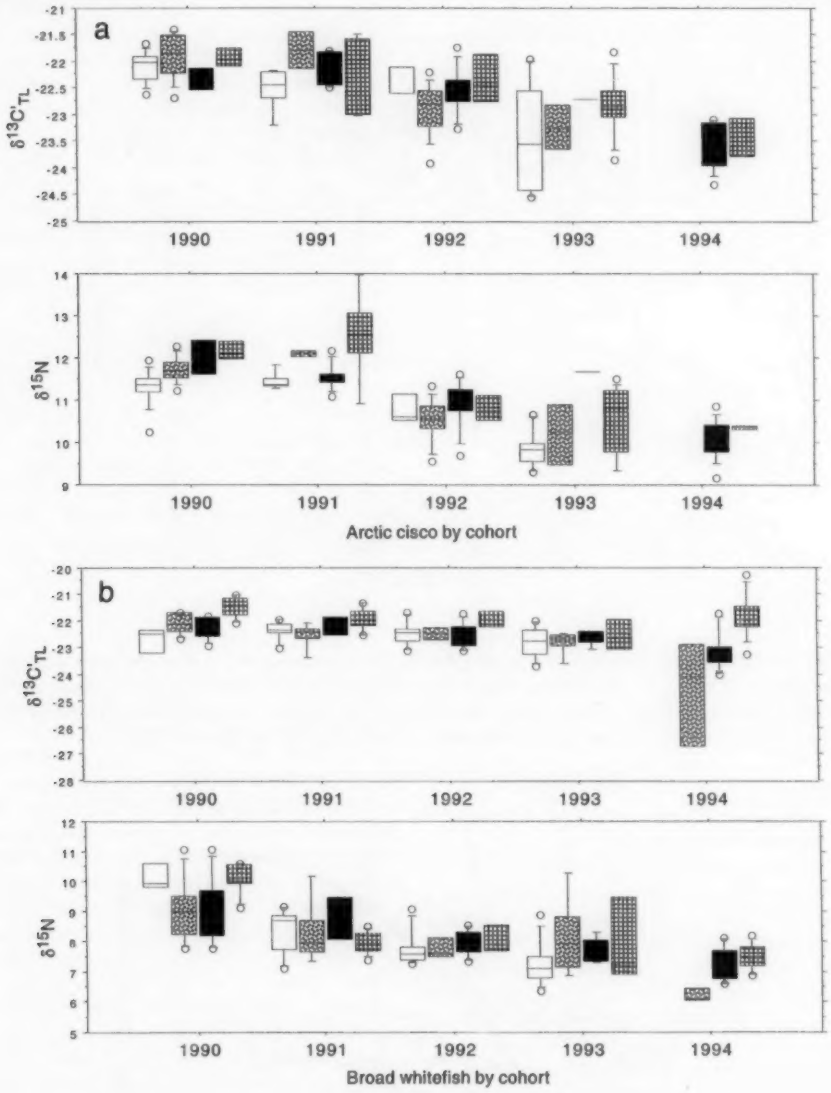
Fig. 6. Carbon and nitrogen isotopic shifts of cohorts (year of birth on *x*-axes) of (*a*) Arctic cisco and (*b*) broad whitefish during four samplings (24 June to 23 July 1994 (open), 11–22 August 1994 (stippled), 23 June to 4 July 1995 (solid), and 14–20 August 1995 (cross-hatched)) shown as box and whisker plots (the five horizontal lines display the 10th, 25th, 50th, 75th, and 90th percentiles), while outliers are shown as symbols. Outliers and percentiles were omitted by computer programming (Statview 4.5, Abacus Concepts, Inc.) for box and whiskers with small *N* as appropriate.



Age 1 and 2 Arctic cisco and broad whitefish (Fig. 6; Table 1) have notable $\delta^{13}C'_{TL}$ and corresponding percent marine carbon estimation differences between the species. Arctic cisco were more negative by ~1‰, suggesting a 5–20% greater affinity for freshwater-derived carbon than broad whitefish (Table 1).

The change in $\delta^{13}C'_{TL}$ between late summer 1994 and early summer 1995 (Fig. 6) suggested a turnover of much of the carbon, probably later in 1994 before entering the rivers. Our observation is consistent with that of Schell (1983) who found $\delta^{13}C$ values in coregonines sampled in October and November that were consistent with continued feeding on marine carbon into the fall. In 1994, the salinity in the Prudhoe Bay area decreased anomalously to low values in late summer when it more typically increases. This may have lengthened the time that these fish spent in the estuary, since the variable that drives them back into the rivers, salinity, became more benign. They could have stayed longer and fed more in late 1994 than is typical. This may have allowed them to change their isotopic composition; otherwise, the late 1994 and early 1995 values of younger cohorts would have been more similar than determined here (compare adjacent stippled and black boxes and whiskers in Fig. 6).

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Table 1. Percent estuarine carbon computed from mean $\delta^{13}C'_{TL}$ values in Fig. 6 using eq. 3 with -28 ± 1.0 and -22 ± 0.5 as the end members.

		Arctic cisco				Broad whitefish			
		1994 sampling		1995 sampling		1994 sampling		1995 sampling	
Year-class	Age (years)	Early season	Late season	Early season	Late season	Early season	Late season	Early season	Late season
1990	4–5	98	102	95	101	88	98	95	109
1991	3–4	92	103	97	96	94	91	97	101
1992	2–3	95	80	91	95	92	92	91	101
1993	1–2		85	88	86	87	86	90	91
1994	0–1			73	76		55	80	106

Note: The accuracy of the estimate based on the $\delta^{13}C'_{TL}$ range of marine fishes of ±8.3% accounts for values >100%.

Our study suggests that, because of the lower trophic position suggested by their $\delta^{15}N$ (Fig. 5), broad whitefish may be able to store energy in a "poor feeding condition," while other species could not. Potentially, measurements of natural stable isotope abundance of fishes in an extreme condition year such as experienced in the Prudhoe Bay region in 1991 could provide evidence of an alternative hypothesis: that broad whitefish shifted feeding to alternative food sources which would in turn cause a shift to different isotopic values because of the change in source of carbon and nitrogen. For example, Fechhelm et al. (1995, 1996) tracked the early- and late-summer condition of individual cohorts of broad whitefish and Arctic cisco over time. Through this analysis, they were able to detect inconsistencies between species and among years in summer energy accumulation. For example, they noted that in the summer of 1991, 75% of Arctic cisco cohorts lost lipid reserves (Fechhelm et al. 1996), while all the broad whitefish cohorts gained lipid reserves (Fechhelm et al. 1995). Fechhelm et al. (1996) noted that 1991 was a very "fresh" year in the Sagavanirktok delta and that Dolly Varden, Arctic flounder, and fourhorn sculpin also exhibited poor condition. They postulated that poor feeding conditions existed throughout the area.

We have shown that anadromous and (or) amphidromous fish have a certain isotopic signature whereas marine and freshwater fishes have another, confirming the freshwater–marine isotopic dichotomy and utilization of ^{13}C-depleted carbon reported by Schell (1983). Within the anadromous and (or) amphidromous group, we can show shifts in trophic level with increase in size, presumably because as fish grow, they are more capable of searching further and accepting different (larger) prey. Natural stable isotope abundance is a technique that could assess changes in the migrational patterns of these fishes, such as changing time of seaward migration to later in life as seen in Dolly Varden. We have also shown that fish at a given size in one year might show a different signature in another year, possibly due to environmental gradients that differed in the two years that enabled those fish to feed in different areas or on different prey. This is especially relevant in the Alaskan Arctic where fishes display widely varying life-history strategies for seasonal feeding and migration to cope with a dynamic and harsh Arctic environment.

Although considerable, environmental impact studies on North Slope fishes have shown little detrimental effect and have contributed considerably to advances in understanding fish life histories in the central Alaskan Beaufort Sea (Gallaway et al. 1997; Wilson and Gallaway 1997). Stable isotope analysis may be an important tool in further advancing this knowledge. Natural stable isotope abundance data provide additional understanding of the feeding ecology of important subsistence and commercial fish and provide a useful tool for analyzing effects of nearshore development in Arctic fishes.

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References

Barnett, B.A. 1994. Carbon and nitrogen isotope ratios of caribou tissues, vascular plants, and lichens from northern Alaska. M.S. thesis, University of Alaska Fairbanks, Fairbanks, Alaska.

Cabana, G., and Rasmussen, J.B. 1994. Modeling food chain structure and contaminant bioaccumulation using stable nitrogen isotopes. Nature (Lond.), **372**: 255–257.

Craig, P.C. 1984. Fish use of coastal waters of the Beaufort Sea: a review. Trans. Am. Fish. Soc. **113**: 265–282.

Craig, P.C. 1989. An introduction to anadromous fishes of the Alaskan Arctic. Biol. Pap. Univ. Alaska, **24**: 27–54.

Craig, P.C., and McCart, P. 1976. Fish use of nearshore coastal waters in the western Arctic: emphasis on anadromous species. *In* Assessment of the arctic marine environment: selected topics. *Edited by* D.W. Hood and D.C. Burrell. Institute of Marine Science, University of Alaska, Fairbanks, Alaska. pp. 361–388.

Craig, P.C., Griffiths, W.R., Johnson, S.R., and Schell, D.M. 1984. Trophic dynamics in an Arctic lagoon. *In* The Alaskan Beaufort Sea, ecosystems and environments. *Edited by* P.W. Barnes,

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D.M. Schell, and E. Reimnitz. Academic Press, Orlando, Fla. pp. 347–380.

DeNiro, M.J., and Epstein, S. 1977. Mechanism of carbon isotope fractionation associated with lipid synthesis. Science (Washington, D.C.), **197**: 261–263.

Fechhelm, R.G., Griffiths, W.B., Wilson, W.J., Gallaway, B.J., and Bryan, J.D. 1995. Intra- and interseasonal changes in the relative condition and proximate composition of broad whitefish from the Prudhoe Bay region of Alaska. Trans. Am. Fish. Soc. **124**: 508–519.

Fechhelm, R.G., Griffiths, W.B., Martin, L.R., and Gallaway, B.J. 1996. Intra- and interseasonal variation in the relative condition and proximate composition of Arctic ciscoes from the Prudhoe Bay region of Alaska. Trans. Am. Fish. Soc. **125**: 600–612.

France, R. 1995. Stable nitrogen isotopes in fish: literature synthesis on the influence of ecotonal coupling. Estuarine Coastal Shelf Sci. **41**: 737–742.

Fry, B. 1988. Food web structure on the Georges Bank from stable C, N, and S isotopic compositions. Limnol. Oceanogr. **33**: 1182–1190.

Fry, B., and Sherr, E.B. 1984. $\delta^{13}C$ measurements as indicators of carbon flow in marine and freshwater ecosystems. Contrib. Mar. Sci. **27**: 13–47.

Gallaway, B.J., Griffiths, W.R., Craig, P.C., Gazey, W.J., and Helmericks, J.W. 1983. An assessment of Colville River delta stock of Arctic cisco (*Coregonus autumnalis*) — migrants from Canada? Biol. Pap. Univ. Alaska, **21**: 4–23.

Gallaway, B.J., Gazey, W.J., Colonell, J.M., Niedoroda, A.W., and Herlugson, C.J. 1991. The Endicott development project — preliminary assessment of impacts from the first major offshore oil development in the Alaskan Arctic. Am. Fish. Soc. Symp. **11**: 42–81.

Gallaway, B.J., Fechelm, R.G., Griffiths, W.R., and Cole, J.G. 1997. Population dynamics of broad whitefish in the Prudhoe Bay region, Alaska. *In* Fish ecology in Arctic North America. *Edited by* J. Reynolds. Am. Fish. Soc. Symp. **19**: 194–207.

Hesslein, R.H., Capel, M.J., Fox, D.E., and Hallard, K.A. 1991. Stable isotopes of sulfur, carbon, and nitrogen as indicators of trophic level and fish migration in the lower Mackenzie River basin, Canada. Can. J. Fish. Aquat. Sci. **48**: 2258–2265.

Hesslein, R.H., Hallard, K.A., and Ramlal, P. 1993. Replacement of sulfur, carbon, and nitrogen in tissue of growing broad whitefish (*Coregonus nasus*) in response to a change in diet traced by $\delta^{34}S$, $\delta^{13}C$, and $\delta^{15}N$. Can. J. Fish. Aquat. Sci. **50**: 2071–2076.

Hobson, K.A., and Welch, H.E. 1992. Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}C$ and $\delta^{15}N$ analysis. Mar. Ecol. Prog. Ser. **84**: 9–18.

Kiriluk, R.M., Servos, M.R., Whittle, D.M., Cabana, G., and Rasmussen, J.B. 1995. Using ratios of stable nitrogen and carbon isotopes to characterize the biomagnification of DDE, mirex, and PCB in a Lake Ontario pelagic food web. Can. J. Fish. Aquat. Sci. **52**: 2660–2674.

Kline, T.C., Jr., Goering, J.J., and Piorkowski, R.J. 1997. The effect of salmon carcasses on Alaskan freshwaters. *In* Freshwaters of Alaska: ecological syntheses. *Edited by* A.M. Milner and M.W. Oswood. Springer-Verlag, New York. pp. 179–204.

Kline, T.C. 1997. Confirming forage fish food web dependencies in Prince William Sound. *In* Forage fishes in marine ecosystems. Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems. Alaska Sea Grant College Program Report No. 97-01. University of Alaska, Fairbanks, Alaska.

Kling, G.W., Fry, B., and O'Brien, W.J. 1992. Stable isotopes and plankton trophic structure in arctic lakes. Ecology, **73**: 561–566.

McConnaughey, T., and McRoy, C.P. 1979. Food-web structure and the fractionation of carbon isotopes in the Bering Sea. Mar. Biol. **53**: 257–262.

McPhail, J.D., and Lindsey, C.C. 1970. Freshwater fishes of northwestern Canada and Alaska. Bull. Fish. Res. Board Can. No. 173.

Minagawa, M., and Wada, E. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}N$ and animal age. Geochim. Cosmochim. Acta, **48**: 1135–1140.

Owens, N.J.P. 1987. Natural variations in ^{15}N in the marine environment. Adv. Mar. Biol. **24**: 389–451.

Schell, D.M. 1983. Carbon-13 and carbon-14 abundances in Alaskan aquatic organisms: delayed production from peat in Arctic food webs. Science (Washington, D.C.), **219**: 1068–1071.

Schell, D.M., and Zieman, P.J. 1989. Natural carbon isotope tracers in Arctic aquatic food webs. *In* Stable isotopes in ecological research. *Edited by* P.W. Rundel, J.R. Ehleringer, and K.A. Nagy. Springer-Verlag, New York. pp. 230–251.

Wada, E., Mizutani, H., and Minagawa, M. 1991. The use of stable isotopes for food web analysis. Crit. Rev. Food. Sci. Nutr. **30**: 361–371.

Wilson, W.J., and Gallaway, B.J. 1997. Synthesis in applied fish ecology: twenty years of studies on effects of causeway development on fish populations in the Prudhoe Bay region, Alaska. *In* Fish ecology in Arctic North America. *Edited by* J. Reynolds. Am. Fish. Soc. Symp. **19**: 326–339.

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Influence of salmon carcasses on stream productivity: response of biofilm and benthic macroinvertebrates in southeastern Alaska, U.S.A.

Mark S. Wipfli, John Hudson, and John Caouette

Abstract: This study was conducted to determine if salmon carcasses (from spawning adults) increased stream biofilm ash-free dry mass (AFDM) and benthic macroinvertebrate abundance in southeastern Alaska, U.S.A. Thirty-six once-through artificial streams were situated along, and received water and drifting invertebrates from, a natural stream. Two treatments (salmon carcass, control) were sampled six times during a 3-month period in a randomized incomplete block design with a 2×6 factorial treatment structure. Additionally, two natural stream sites were sampled once for biofilm and macroinvertebrates, one site receiving 75 000 adult salmon migrants during 1996 and the other upstream of spawning salmon. While biofilm AFDM was 15 times higher in carcass-enriched reaches of Margaret Creek, there were no detectable treatment differences in the artificial streams. Total macroinvertebrate densities were up to eight and 25 times higher in carcass-enriched areas of artificial and natural streams, respectively; Chironomidae midges, *Baetis* and *Cinygmula* mayflies, and *Zapada* stoneflies were the most abundant taxa. The increased biofilm in Margaret Creek and macroinvertebrate abundance in both systems suggest that salmon carcasses elevated freshwater productivity. This marine-based positive feedback mechanism may be crucial for sustaining aquatic–riparian ecosystem productivity and long-term salmonid population levels.

Résumé : La présente étude visait à déterminer si les carcasses de saumon (géniteurs adultes) augmentaient la masse sèche exempte de cendres du film biologique d'un cours d'eau et l'abondance des macroinvertébrés benthiques dans le sud-est de l'Alaska (É.-U.). Trente-six cours d'eau artificiels à circulation ouverte ont été créés le long d'un cours d'eau naturel qui les alimentait en eau et en invertébrés à la dérive. Deux groupes de traitement (carcasse de saumon, témoin) ont été échantillonnés six fois pendant une période de trois mois dans le cadre d'un plan expérimental en blocs aléatoires incomplets avec une structure de traitement factorielle de 2×6. En outre, on a prélevé des échantillons de film biologique et de macroinvertébrés dans deux sites de cours d'eau naturels, un site recevant 75 000 saumons adultes migrants en 1996 et l'autre situé en amont de la frayère. Alors que le film biologique de masse sèche exempte de cendres était 15 fois plus élevé dans les tronçons du ruisseau Margaret enrichis par les carcasses, il n'y avait aucune différence de traitement décelable dans les cours d'eau artificiels. La densité totale de macroinvertébrés était respectivement jusqu'à huit et 25 fois supérieure dans les zones enrichies de carcasses des cours d'eau artificiels et naturels; les moucherons chironomidés, les éphémères *Baetis* et *Cinygmula* et les perles *Zapada* étaient les groupes les plus abondants. L'accroissement du film biologique dans le ruisseau Margaret et de l'abondance des macroinvertébrés dans les deux systèmes semblent indiquer que les carcasses de saumon font augmenter la productivité des eaux douces. Ce mécanisme de rétroaction positive provenant du milieu marin peut être critique pour le maintien de la productivité de l'écosystème aquatique et riverain et les niveaux de population de salmonidés à long terme. [Traduit par la Rédaction]

Introduction

Aquatic productivity is often governed by dissolved organic carbon (DOC) and nutrient levels (Warren et al. 1964; Borchardt 1996; Stockner and MacIsaac 1996). Small increases in their concentrations can dramatically increase primary production (Stockner and Shortreed 1978; Peterson et al. 1993; Perrin et al. 1987), heterotrophic activity (Sobczak 1996), and secondary production (Peterson et al. 1993; Stockner and MacIsaac 1996). These "bottom-up" effects can reach upper trophic levels (Mundie et al. 1991; Lamberti 1996) including predatory fishes (Stockner and MacIsaac 1996; Kyle et al. 1997). DOC added as sucrose to a western Oregon stream increased bacterial growth, aquatic insect abundance, and predation by and subsequent production of coastal cutthroat trout (*Oncorhynchus clarki*) (Warren et al. 1964). Nitrogen and phosphorus additions to a small coastal stream increased periphyton standing crop and steelhead trout (*Oncorhynchus mykiss*) and coho salmon (*Oncorhynchus kisutch*) fry size in British Columbia (Johnston et al. 1990). These nutrients, artificially added to lakes, also increased sockeye (*Oncorhynchus nerka*) and coho salmon production in Alaska (Kyle et al. 1997) and sockeye production in British Columbia (Stockner and MacIsaac 1996). Peterson et al. (1993) detected bottom-up effects up through several trophic levels including Arctic grayling (*Thymallus arcticus*) from phosphorus additions to a tundra stream in Alaska.

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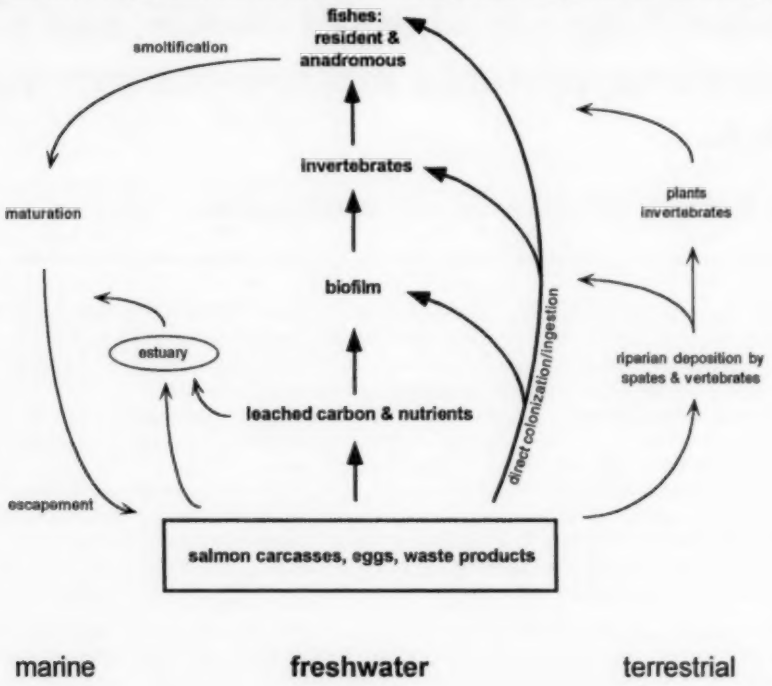
Fig. 1. Proposed major trophic pathways influenced by anadromous salmonids in freshwater ecosystems. Bold text and arrows represent energy flow within freshwater food webs; lightface text and arrows show the major links with marine and terrestrial systems.



Returns of salmon and other anadromous species may be important for aquatic–riparian ecosystem productivity (Levy 1997), particularly in nutrient-poor systems characteristic of western North America (Stockner and MacIsaac 1996), including Alaska (Peterson et al. 1993; Kyle et al. 1997). Fish carcasses and eggs can contribute nutrients and DOC (Mathisen et al. 1988; Schuldt and Hershey 1995; Kyle et al. 1997) that stimulate primary production leading to possible elevated productivity of higher trophic levels. Additionally, fish and other animal carcasses may act as "slow-release" fertilizers providing nutrients through much of the year (Parmenter and Lamarra 1991). Although there is good evidence that marine-derived nutrients (e.g., nitrogen) are present in some aquatic food webs that receive annual returns of anadromous fishes (Bilby et al. 1996; Johnston et al. 1997; Kline et al. 1997), little information exists about whether marine-derived nutrients or carbon increase aquatic productivity.

Salmonid escapements appear to be at or near historic levels in southeastern Alaska and parts of western Canada (Baker et al. 1996; Slaney et al. 1996), unlike other regions of the world (Wheeler and Sutcliffe 1990; Nehlsen et al. 1991). Spawning adults deposit marine-based carbon and nutrients in freshwater via excretion, eggs, and adult carcasses (Mathisen et al. 1988; Kline et al. 1997) and may have important consequences for aquatic–riparian productivity. Increased carbon and nutrients should stimulate biofilm (i.e., mixed assemblage of autotrophic and heterotrophic microbes embedded in a glycoprotein polysaccharide matrix attached to stream substrates) production (Fig. 1). More biofilm means more food directly for invertebrate scrapers and collectors and indirectly for predatory invertebrates. These bottom-up effects should continue passing through the food web reaching higher trophic levels including juvenile salmonids and other predatory fishes, leading to their increased production (Fig. 1). Determining all functions of salmonid escapements in freshwater–riparian ecosystems is crucial for understanding marine–freshwater–terrestrial linkages (Fig. 1) for fisheries and ecosystem management. This information is critical for managing fish escapements in the Pacific Northwest and globally, and may be particularly important in parts of the world for restoring suppressed salmon stocks.

The objectives of this study were to assess the influence of salmon carcasses on aquatic productivity through changes in biofilm ash-free dry mass (AFDM) and benthic macroinvertebrate abundance in artificial and natural streams in southeastern Alaska. We tested the hypothesis that material leached from salmon carcasses increase biofilm AFDM and benthic macroinvertebrate abundance in lotic ecosystems.

Methods

Study site

The study took place within the Margaret Creek watershed on Revillagigedo Island near Ketchikan, Alaska. The climate is maritime, cool, and moist; precipitation can exceed 500 cm·year^{-1} in some areas. The Margaret watershed is 38 km^2 and supports anadromous sockeye, pink (*Oncorhynchus gorbuscha*), chum (*Oncorhynchus keta*), and coho salmon, steelhead and cutthroat trout, and Dolly Varden (*Salvelinus malma*). A fish ladder installed in 1990 around a natural fish barrier (i.e., waterfalls that historically prevented upstream movement of fishes) about 1 km upstream of salt water has

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provided anadromous fishes with access to upstream reaches of the watershed. Resident fishes included kokanee salmon (*O. nerka*), cutthroat trout, and rainbow trout (*O. mykiss*), Dolly Varden, prickly sculpin (*Cottus asper*), and threespine stickleback (*Gasterosteus aculeatus*). Juvenile sockeye salmon stocking has occurred in Margaret Lake within the watershed between 1988 and 1994 (McCurdy and Bryant 1997).

Experiments were conducted from 18 August through 12 November. Spawning salmon densities were greatest from July through October 1996. About 75 000 adult pink, chum, coho, and sockeye salmon returned to Margaret Creek during 1996, and 25 000 of those passed through the fish ladder into upper parts of the watershed (S. McCurdy, Pacific Northwest Research Station, USDA Forest Service, 2770 Sherwood Lane, Juneau, AK 99801, U.S.A., personal communication). Pink salmon were the most abundant anadromous species.

Mesocosm experiment

The mesocosm consisted of 36 straight once-through artificial stream channels, each 250 cm long × 18 cm wide, constructed in the riparian forest along Spike Creek, a second-order tributary of Margaret Creek. Stream water containing naturally drifting invertebrates was gravity-fed through black polyethylene pipes from a nonanadromous portion of Spike Creek (immediately upstream of a waterfall) to a header tank. Water was then delivered from the header tank to each channel through T-valves, passed through the channels, and then into an outflow flume that collected and carried it back to the natural stream. Six channels were constructed per table, on six tables.

Each channel was divided into three experimental sections: a 60-cm pool for treatments (salmon carcass or no carcass), a 45-cm pool habitat, and a 85-cm riffle habitat, all containing mineral substrata (collectively 7 L of 4-cm-diameter gravel and 5 L of 4- to 20-cm-diameter gravel) from the natural stream. A 15.0 × 15.0 cm unglazed clay tile was placed at the downstream end of each riffle habitat for sampling biofilm. Invertebrates could freely drift in and out of channels throughout the experiment and immediately began colonizing substrata in channels via drift from the natural stream. The benthic macroinvertebrate community composition in these channels normally resembles the Spike Creek community within 1–2 weeks after stream water begins flowing through channels (M. Wipfli, Pacific Northwest Research Staion, Juneau, Alaska, unpublished data); some taxa with a low propensity to drift (e.g., cased Trichoptera) were less frequent in artificial streams versus the natural stream. Discharge through each channel was 0.52 ± 0.03 $L \cdot s^{-1}$ throughout the experiment. Water temperature in the mesocosm, logged at continuous 1-h intervals, averaged 7.5°C (range 1.6–13.3°C) during the experiment.

Two treatments were applied: single salmon carcass and control (no carcass). Twenty-one live female pink salmon containing eggs were collected from Margaret Creek on 18 August, killed, and weighed (range 1.4–1.8 kg wet mass). Stream water passed through the channels for 2 days, and then, one fish was placed in each of 18 channels, in three randomly selected channels per table, for all six tables. Carcasses were secured with monofilament line in the upstream pool. Discharge of 0.52 $L \cdot s^{-1}$ through the channels resulted in 3.2 kg carcass wet mass·L $water^{-1} \cdot s^{-1}$ (3.6–4.7 kg carcass wet mass·m^{-2}). Fiberglass screen was placed beneath each carcass to facilitate its removal for dry mass determinations. The three remaining fish were weighed wet and then oven-dried at 80°C and reweighed to calculate a mean dry mass to wet mass ratio. This value (0.28) was used to estimate dry mass loss for carcasses placed in channels. Pools of all channels were covered with Plexiglas® fastened to channel tops to protect carcasses from bears and other scavengers.

Biofilm and benthic macroinvertebrates were sampled six times during the 87-day experiment. Six randomly chosen channels (one carcass replicate and one control replicate from each of three tables) were destructively sampled during each of the six sampling events.

Biofilm

Biofilm was collected from a 56-cm^2 portion of the upper surface of the unglazed clay tiles for AFDM measurements. Tiles were removed from channels, scraped, brushed, and flushed with water into Nalgene® bottles. Individual samples were refrigerated while at the field site and then transported to the laboratory and filtered, oven-dried, weighed, ashed at 500°C, and reweighed for calculation of AFDM (see Steinman and Lamberti 1996).

Macroinvertebrates

Benthic macroinvertebrates were collected directly from carcasses and from mineral substrata in both pool and riffle habitats. They were also counted on the top surfaces of the clay tiles, without physically disturbing the tiles, every few days throughout the experiment.

Riffle- and pool-dwelling macroinvertebrates were collected on two consecutive days during each sampling period. Using our hands, we agitated riffle substrata three times for 4 min each per channel; dislodged invertebrates were collected in 250-μm Nitex® nets that were attached to channel outflows. Pool-dwelling macroinvertebrates were sampled similarly on the following day. After invertebrates were collected from the substrata, a subsample of macroinvertebrates representative of all visible taxa was collected from the surface of each carcass or from its associated microbial layer. Macroinvertebrates were sorted, identified to the lowest reliable taxon, and, for noncarcass taxa, counted. Finally, carcasses were removed, dried at 80°C, and weighed to determine their dry mass loss during the experiment. To do this, we estimated their initial dry mass by multiplying 0.28 (dry mass to wet mass ratio described above) by their starting wet mass and subtracting their final dry mass to give dry mass lost.

Natural stream experiment

Although this study centered around the mesocosm, we sampled a natural stream to determine whether patterns in biota abundance occurring in a natural system were similar to those in the more controlled and statistically rigorous artificial streams. Even though we carefully chose study sites that minimized natural between-site differences, some obvious differences existed. A 55-ha lake separated the two study reaches. While both sites contained predominantly gravel and cobble, the downstream habitat on average had larger substrate, was higher gradient, and was about twice as wide as the upstream site. Water temperature, logged at continuous 1-h intervals, averaged 8.8°C (range 4.4–12.9°C) and 10.6°C (range 6.3–16.5°C) in the upstream and downstream reaches, respectively, between 26 August and 23 October. We collected no additional physical or chemical data from Margaret Creek.

Baseflow stream discharge recorded on 14 August was 752 and 1539 $L \cdot s^{-1}$ in the upstream and downstream reaches, respectively. At these discharges and 75 000 salmon, the "carcass concentration" in upper and lower Margaret Creek was between 0 and 80 kg carcass wet mass·L $water^{-1} \cdot s^{-1}$, respectively (relative to 3.2 kg carcass wet mass·L $water^{-1} \cdot s^{-1}$ in the artificial streams). Actual carcass concentration in lower Margaret Creek was probably much less than 80 kg carcass wet mass·L $water^{-1} \cdot s^{-1}$ because many fish are eaten by vertebrates (Willson and Halupka 1995) or get flushed downstream into the estuary (M.S. Wipfli, personal observation).

Biofilm

A biofilm sample was collected from each of four stones from each of two Margaret Creek sites (= treatments) within riffle habitats on 20 October. One site was in a lower reach that contained the highest concentration of salmon carcasses (carcass-enriched treatment), and the other was upstream of spawning anadromous salmonids (control treatment). Stones were selected based on location (midchannel within a riffle), size (as large as possible, yet small enough for one person to carry from the stream), and shape (slightly flattened to facilitate sampling). A 56-cm^2 patch on the upper surfaces of each stone was scraped with a razor blade, brushed with a toothbrush, and

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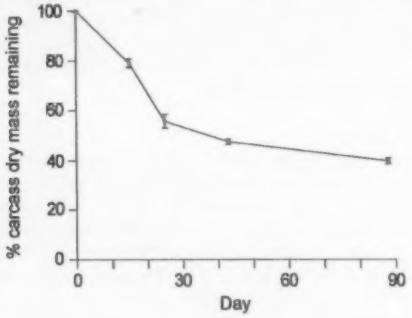
Fig. 2. Mean salmon carcass dry mass remaining in artificial channels throughout the 87-day mesocosm experiment. Error bars represent 1 SEM.



then flushed with water into individual plastic bags and refrigerated. Samples were processed for AFDM as described earlier.

Macroinvertebrates

Benthic macroinvertebrates were collected on 23 October from seven stones in a similar fashion as biofilm samples. Invertebrates within a 100-cm^2 area were brushed from the top surface of each stone, flushed with water through a 250-μm sieve, placed in 95% ethanol, identified, and counted.

Experimental design and statistical analyses

Response variables for analyses were biofilm AFDM and benthic macroinvertebrate abundance in both natural stream and mesocosm experiments. Macroinvertebrates were identified to the lowest reliable taxa and analyzed at two general taxonomic resolutions: total invertebrates (all taxa combined) and either family or genus.

An incomplete block design was used with a 2×6 factorial treatment structure in the mesocosm and data analyzed with PROC GLM (SAS Institute Inc. 1989). Power analyses indicated that this design would provide the most information, while optimizing statistical power, to test hypotheses. We performed *t*-tests on Margaret Creek data. All count data (benthic macroinvertebrates) were transformed via natural logarithm to meet ANOVA assumptions (e.g., nonhomogeneous variance).

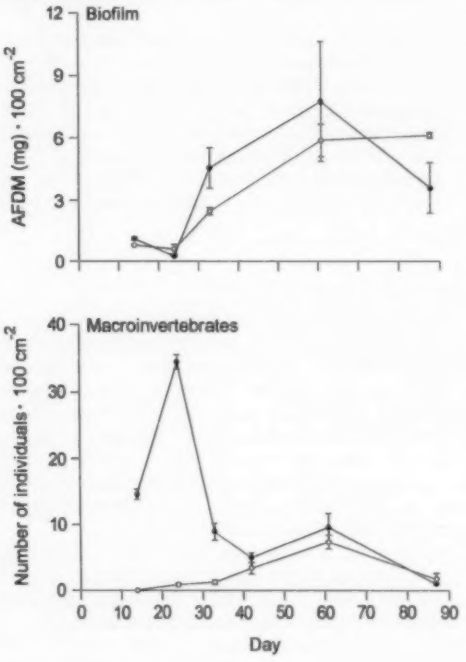
We caution that an upstream–downstream comparison within one stream (Margaret Creek) is pseudoreplication (Hurlbert 1984) and does not provide a means of separating treatment factors (carcasses, no carcasses) from other variables (e.g., gradient, substrate, discharge, lake effects). Nonetheless, this approach did provide the opportunity to determine if differences in invertebrate abundance and biofilm AFDM in the natural stream corresponded to the responses measured in the artificial channels.

Results

Mesocosm experiment

Salmon carcasses lost 60% of their original dry mass by the end of the 3-month experiment; mass loss was most rapid within the first 25 days (Fig. 2). They apparently lost mass through several processes, including microbial and invertebrate processing and dissolution and leaching. They became covered with invertebrates and a thick, fuzzy-looking microbial layer and slowly deflated through time; a cream-colored amorphous suspension was seen leaking from the carcasses. Macroinvertebrates were also seen burrowing into carcasses.

Fig. 3. Mean biofilm AFDM and benthic macroinvertebrate densities that colonized clay tiles in artificial channels, contrasting carcass-enriched (solid circles) and control (open circles) treatments, throughout the 87-day mesocosm experiment. Error bars represent 1 SEM.



As a result of carcasses being placed in pools, we observed no physical breakdown (e.g., abrasion by water or sediments).

Biofilm

Although we observed a thicker mat of biofilm on carcass-treatment tiles during the experiment, no significant differences in AFDM were found between treatments (Fig. 3, $p > 0.05$). While the lack of AFDM differences could have been due to absence of treatment effects, it appeared that grazers and physical sloughing removed much of the biofilm layer as it developed, potentially masking treatment effects. Significantly more macroinvertebrates were counted on the tiles in channels containing carcasses, especially during the first 30 days (Fig. 3, $p < 0.001$), demonstrating that they were probably responding to an elevated food resource (i.e., biofilm) absent in the control channels.

Macroinvertebrates

Benthic macroinvertebrate densities were significantly higher in both pool (Fig. 4; Table 1, $p < 0.001$) and riffle (Fig. 5; Table 1, $p < 0.001$) habitats in the carcass-enriched channels. Total macroinvertebrate number was eight times higher 25 days into the experiment in both habitats (Figs. 4 and 5). By the end of the study, densities were still higher in the carcass-enriched channels. Chironomid midges (Diptera: Chironomidae) were the most abundant taxon in both pool and riffle habitats, comprising 85 and 35% (averaged for both carcass and control channels) of the total number, respectively. This

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family comprised numerous genera (Table 1). *Paraleptophlebia* (Ephemeroptera: Leptophlebiidae) (4%) and *Zapada* (Plecoptera: Nemouridae) (3%) were the next most abundant taxa in pool habitats (Fig. 4), while *Baetis* (Ephemeroptera: Baetidae) (22%) and *Zapada* (17%) were the next most common insects in riffle habitats (Fig. 5), followed by *Cinygmula* (Ephemeroptera: Heptageniidae) (9%), Capniidae/Leuctridae (Plecoptera) complex (5%), and black flies (Diptera: Simuliidae) (4%). Capniidae/Leuctridae and Simuliidae were the only relatively common taxa (>3% abundance) that did not show a density increase in the presence of salmon carcasses (Fig. 5; Table 1, $p > 0.05$). The densities of remaining less common taxa in both pool and riffle habitats also generally increased with carcass enrichment (Table 1).

Additionally, the temporal colonization patterns were different among taxa. Chironomidae and *Baetis* were the earliest colonizers of the carcass-enriched habitat, followed by *Zapada*, then *Cinygmula* and *Paraleptophlebia*, and finally capniid and leuctrid stoneflies (Figs. 4 and 5). These patterns were not apparent in the control treatment.

Several taxa were observed on carcasses, including *Brillia*, *Corynoneura*, *Polypedilum*, and *Pseudodiamesa* (Diptera: Chironomidae), *Zapada*, *Ameletus* (Ephemeroptera: Ameletidae), and *Onocosmoecus* and *Ecclisomyia* (Trichoptera: Limnephilidae). Chironomidae were observed burrowing into carcasses and were abundant within the salmon tissue after 30 days.

Natural stream experiment

Biofilm and macroinvertebrates

Biofilm AFDM collected from stone surfaces was significantly higher in the carcass-enriched portion of Margaret Creek, about 15 times greater than in the upstream "control" reach (Fig. 6, $p < 0.001$). Benthic macroinvertebrate densities were also significantly higher in the carcass-enriched stream reaches than in the control reaches (Fig. 6, $p < 0.001$). As with the mesocosm experiment, Chironomidae, composed of *Cricotopus*, *Eukiefferella*, *Paratrissocladius*, and *Pseudosmittia*, were the most abundant taxa. *Baetis* was the second most abundant.

Discussion

This study generally supports the hypotheses that salmon carcasses increase freshwater biofilm and benthic macroinvertebrate abundance, suggesting that carcass-derived nutrients or carbon elevate stream productivity. Our results agree with previous freshwater nutrient-enrichment studies conducted in western North America in which artificially added inorganic nutrients, particularly nitrogen and phosphorus, and organic matter elevated biological activity at several trophic levels (Warren et al. 1964; Peterson et al. 1993; Lamberti 1996; Stockner and MacIsaac 1996).

Although treatment differences were not detected with biofilm AFDM in the artificial channels, we believe that the biofilm may have responded to carcass enrichment, as seen in the natural stream. We observed more sloughing in the artificial versus natural streams, possibly due to different microlayer conditions (e.g., turbulence, velocity, sediment load) that would affect sloughing rates. Also possible was a more rapid biofilm recolonization following sloughing in the natural stream from higher carcass concentrations there (i.e., more stream nutrients) (with about 80 versus 3.2 kg carcass wet mass·L water^{-1}·s^{-1} in the natural and artificial streams, respectively). On the other hand, the differences between treatments in Margaret Creek may have been a function of confounding variables including background nutrient levels (likely influenced by Margaret Lake), stream temperature, and light levels (due to different channel widths and riparian shading) between the upstream and downstream sites.

Fig. 4. Mean benthic macroinvertebrate densities in the pool habitat within artificial channels, contrasting carcass-enriched (solid circles) and control (open circles) treatments, throughout the 87-day mesocosm experiment. These taxa represent the three most abundant groups in the pool habitat. Error bars represent 1 SEM.

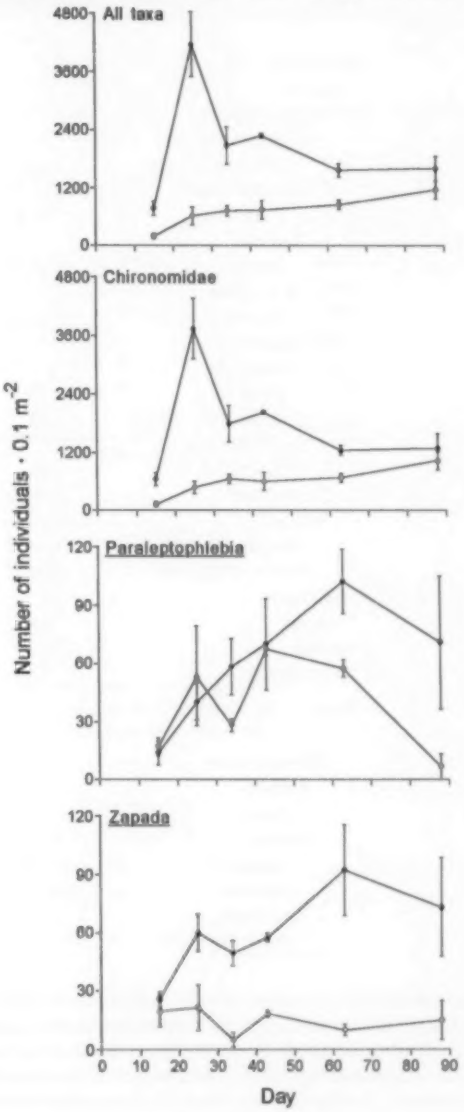

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Table 1. Percent relative abundance, mean natural logarithm transformed abundance (no. · m^{-2}), and ANOVA results of benthic macroinvertebrates collected from pool and riffle habitats in artificial streams from carcass and control treatments.

Taxon	Functional feeding group[a]	% relative abundance[b]	Treatment means[c]		ANOVA	
			Carcass	Control	MS_{error}[d]	p
		Pool				
Arthropoda						
Insecta						
Ephemeroptera						
Leptophlebiidae						
Paraleptophlebia	c-g	3.5	6.11	5.14	1.37	0.0218
Heptageniidae[e]	c-g, sc	0.2	2.70	0.14	1.31	<0.0001
Cinygmula	c-g, sc	0.6	4.36	1.47	2.81	<0.0001
Baetidae						
Baetis[f]	c-g, sc	0.5	3.37	1.82	3.30	0.0187
Ameletidae						
Ameletus validus	c-g, sc	0.3	3.02	0.65	2.83	0.0005
Plecoptera						
Nemouridae						
Zapada[g]	sh	2.7	6.28	4.53	0.88	<0.0001
Capniidae/Leuctridae	sh	1.2	4.95	4.32	1.09	0.0854
Chloroperlidae						
Sweltsa	pr	0.4	2.27	3.31	3.80	0.1257
Trichoptera[h, i]	Several	0.8	4.07	3.22	2.61	0.1334
Diptera[j]	Several	0.7	4.39	4.05	0.81	0.2800
Chironomidae (l)[k]	Several	85.1	9.62	8.43	0.13	<0.0001
Chironomidae (p)[l]	Several	2.3	4.24	2.75	1.01	0.0003
Arachnida						
Acari	om	0.2	2.98	1.92	2.96	0.0804
Annelida						
Oligochaeta	c-g	1.3	4.32	4.25	1.14	0.8363
All taxa		100.0	9.79	8.70	0.07	<0.000 1
		Riffle				
Ephemeroptera						
Baetidae						
Baetis[f]	c-g, sc	21.8	7.05	5.32	0.42	<0.0001
Heptageniidae[e]	c-g, sc	1.9	4.72	3.34	0.39	<0.0001
Cinygmula	c-g, sc	9.0	6.07	4.89	0.15	<0.0001
Epeorus[m]	c-g, sc	0.2	2.06	0.89	1.40	0.0079
Ameletidae						
Ameletus validus	c-g, sc	1.2	3.35	2.15	0.89	0.0011

Soluble material from the salmon carcasses was rapidly released into stream water, apparently microbial and invertebrate mediated, as evidenced by the carcass mass loss (in the absence of apparent physical breakdown). Similar to other animal flesh, salmon contain proteins, fats, and other biochemicals (Mathisen et al. 1988), comprising potential productivity-limiting carbon, nitrogen, and phosphorus (Borchardt 1996; Stockner and MacIsaac 1996). Some combination of these stream-leached compounds appeared to influence biofilm and subsequently had a rapid and dramatic effect on benthic macroinvertebrate abundance in this study.

Although results from Margaret Creek need to be interpreted with caution (due to possible confounding variables as discussed earlier), we did observe the same general pattern in the biota — higher abundance in carcass-enriched stream reaches — in the natural and artificial streams (except for the artificial stream tile-colonized biofilm). This suggests that carcass-leached material may have had a similar effect on Margaret Creek benthos as it did in the mesocosm.

In addition to chemical processing through dissolution of tissue, biological processing of carcasses was apparent and may be ecologically important. Carcasses, with their associated microbial community, were colonized by macroinvertebrates in this study and may be an important food source for these scavengers. Macroinvertebrates (most commonly chironomid midge larvae) were seen on and penetrating into carcasses and were collected from carcasses after the experiment began; they became more abundant on carcasses through time. Kline et al. (1997) found several benthic macroinvertebrate taxa associated with salmon carcasses in interior Alaska streams, commonly several species of limnephilid caddisflies; these larvae were enriched with marine-derived nutrients. Minakawa (1997) also observed insects feeding on salmon tissue, and exhibiting higher growth rates, in Washington. In

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Table 1 (*concluded*).

Taxon	Functional feeding group[a]	% relative abundance[b]	Treatment means[c]		ANOVA	
			Carcass	Control	MS_{error}[d]	p
Leptophlebiidae						
Paraleptophlebia	c-g	0.5	1.44	3.30	1.64	0.0003
Ephemerellidae						
Drunella[n]	sc	0.2	2.29	0.45	1.65	0.0004
Plecoptera						
Nemouridae						
Zapada[g]	sh	16.5	7.05	5.49	0.07	<0.0001
Capniidae/Leuctridae	sh	5.1	4.96	4.38	0.85	0.0768
Chloroperlidae						
Sweltsa	pr	0.2	1.80	1.02	1.22	0.0496
Trichoptera[e, i]	Several	0.6	2.60	2.21	2.56	0.4662
Diptera[j]	Several	0.5	3.07	2.44	0.92	0.0547
Chironomidae (l)[p]	Several	35.4	7.41	5.78	0.13	<0.0001
Chironomidae (p)	Several	2.5	3.65	2.75	0.55	<0.0001
Simuliidae[q]	c-f	4.2	5.32	5.12	0.17	0.1494
All taxa		100.0	8.86	7.36	0.03	<0.0001

[a]c-g, collector–gatherer; sc, scraper; sh, shredder; pr, predator; om, omnivore; c-f, collector–filterer (Merritt and Cummins 1996).

[b]Relative abundance as a percentage of all macroinvertebrates pooled across both treatments.

[c]$n = 18$.

[d]df = 19.

[e]*Epeorus* and *Cinygmula* ≤2 mm long.

[f]*Baetis bicaudatus*, *B. tricaudatus*.

[g]*Zapada cinctepes*, *Z. columbiana*.

[h]*Ecclisomyia*, *Onocosmoecus unicolor*, *Micrasema*, *Glossosoma*.

[i]*Rhyacophila*, *Polycentropus*, *Wormaldia*, *Psychoglypha*.

[j]Empididae (*Clinocera*, *Oreogeton*), Tipulidae (believed to be *Raphidolabina*, *Dicranota*), Ceratopogonidae.

[k]*Corynoneura*, *Stilocladius*, *Brillia*, *Heterotrissocladius*, *Psuedodiamesa*, *Polypedilum*, *Macropelopia*, *Parametriocnemus*, *Micropsectra*, *Paramerina*, *Zavrelimyia*, *Eukiefferiella*, *Rheocricotopus*, *Heterotanytarsus*, *Paraphaenocladius*, *Chironomus*, *Phaenopsectra*; l, larvae.

[l]p, pupae.

[m]*Epeorus* spp. (believed to be *deceptivus*), *E. longimanus*, *E. grandis*.

[n]*Drunella doddsi*, *Drunella* spp. (believed to be *grandis*).

[o]*Glossosoma*, *Parapsychae elsis*, *Ecclisomyia*, *Onocosmoecus unicolor*.

[p]*Eukiefferiella*, *Corynoneura*, *Stilocladius*, *Brillia*, *Rheocricotopus*, *Psuedodiamesa*, Thienemannimyia group, *Macropelopia*, *Parametriocnemus*, *Micropsectra*, *Paramerina*, *Tvetenia*, *Heterotrissocladius*, *Paraphaenocladius*, *Polypedilum*.

[q]*Simulium pugetense*, *S. nebulosum*, *Stegopterna* sp.

Minnesota where salmon are not endemic, scavenging invertebrates were uncommon on salmon carcasses, with a shredding stonefly the most apparent (Schuldt and Hershey 1995).

This elevated invertebrate abundance from salmon carcass derived carbon or nutrients likely means more energy (via greater prey abundance) reaching upper trophic levels, including juvenile salmonids and other predators in both the aquatic and riparian systems (Fig. 1). Increased fish production is likely if these bottom-up forces transfer through the food web to upper (predator) levels. Food often appears to limit salmonid production in streams in western North America (Chapman 1966). Bilby et al. (1996) recorded increased juvenile coho salmon growth rates in a Washington stream after salmon began to spawn. Michael (1995) also noted higher juvenile coho salmon growth rates in a stream with spawning pink salmon than in one without.

These results have important implications for fisheries management. If freshwater ecosystems rely on this annual salmon-derived nutrient pulse for sustaining productivity, then managing salmon escapements at or above a certain threshold may be crucial. These marine-derived nutrients may be especially important for the naturally oligotrophic freshwater systems characteristic of the Pacific Northwest (Perrin et al. 1987; Stockner and MacIsaac 1996), providing a positive feedback mechanism that helps sustain regionally productive salmonid fisheries.

Another important fishery management implication concerns fish pass or "ladder" construction, a tool intended to "enhance" selected anadromous species. These artificial fish passes built at natural barriers (e.g., waterfalls) provide anadromous fishes access to previously unavailable upstream habitats. Concerns exist about possible negative effects of introduced anadromous species on native resident fishes (i.e., through competition or predation) in southeastern Alaska

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Fig. 5. Mean benthic macroinvertebrate densities in the riffle habitat within artificial channels, contrasting carcass-enriched (solid circles) and control (open circles) treatments, throughout the 87-day mesocosm experiment. These taxa represent the six most abundant groups in the riffle habitat. Error bars represent 1 SEM.

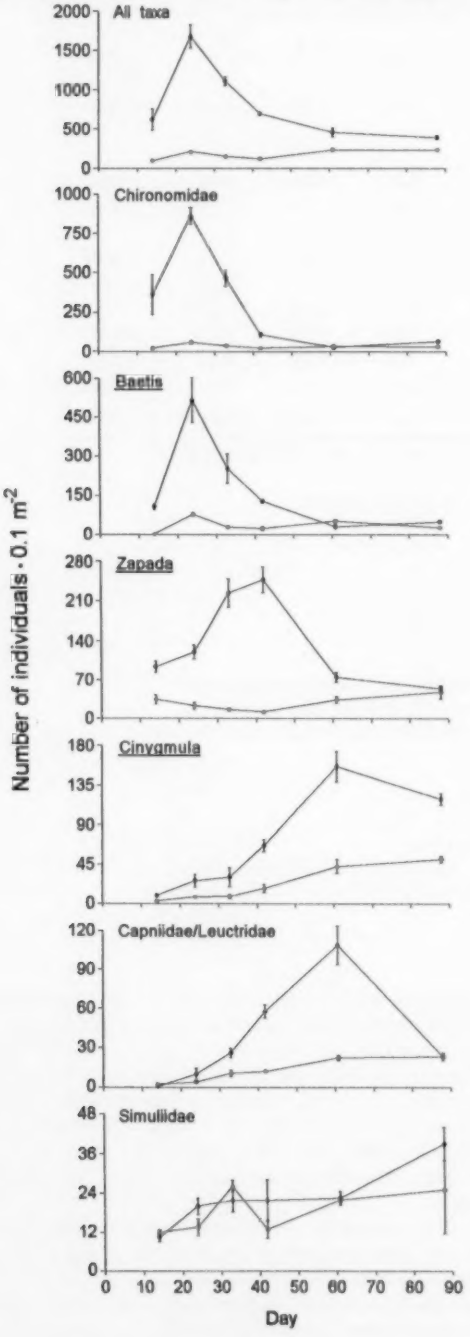
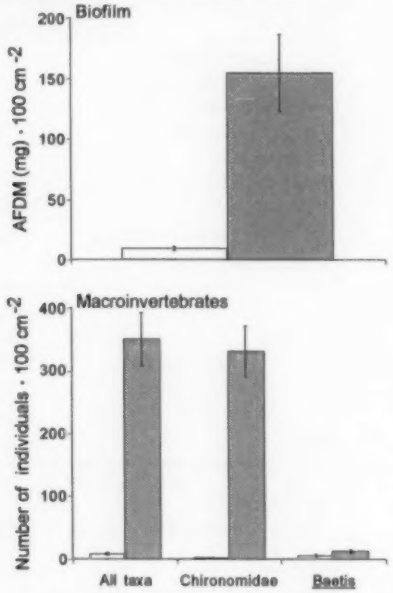


Fig. 6. Mean biofilm AFDM and benthic macroinvertebrate densities on stone surfaces within Margaret Creek, contrasting downstream carcass-enriched (shaded bars) and upstream control (open bars) riffle habitats. Error bars represent 1 SEM.



(McCurdy and Bryant 1997). Alternatively, this annual nutrient influx via anadromous fishes may have beneficial effects on resident fishes by elevating aquatic production, thereby providing more prey and less competition. Therefore, elevated freshwater food web productivity through anadromous species introductions may serve to increase both anadromous and resident fish production. Introduced anadromous salmon have not had a noticeable negative effect on resident fishes in the Margaret system (McCurdy and Bryant 1997), where this study was conducted. Theoretically, positive effects from enrichment could negate effects from competition or predation.

These results may also have important implications for restoring impoverished stocks in regions of the world where freshwater habitat destruction or overfishing has depleted runs. If freshwater ecosystems have historically depended on this annual influx of marine-derived material, they may first require elevated carbon or nutrient levels to boost trophic productivity before they can successfully recruit and sustain desired levels of fish production. Restoring suppressed stocks may initially require artificially elevating nutrients concurrently with other restoration strategies (i.e., juvenile stocking) until spawning salmon reach numbers that are sufficient for self-fertilization of the system. This strategy appeared successful in some Alaskan lakes where nutrient enrichment (nitrogen and phosphorus), together with juvenile salmon stocking, increased salmon production in systems that were experiencing depressed adult returns (Kyle et al. 1997). However, long-term effects (e.g., over decades) remain to be seen. Alternatively, even low returning adult numbers (of depleted stocks) may progressively fertilize a system through time, possibly enabling impaired systems to achieve naturally their trophic capacity.

A more advanced understanding of the role that anadromous salmonids play in freshwaters and associated terrestrial

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ecosystems is crucial for a more holistic approach to fisheries and ecosystem management. This annual nutrient influx via anadromous species may be critically important for sustaining productivity and biodiversity, both regionally and globally. Long-term sustainability may hinge on managing escapements to sustain trophic productivity of freshwater habitat. Understanding the significance of this nutrient influx should help the management of both healthy and impoverished stocks throughout the world.

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References

Baker, T.T., Wertheimer, A.C., Burkett, R.D., Dunlap, R., Eggers, D.M., Fritts, E.I., Gharrett, A.J., Holmes, R.A., and Wilmot, R.L. 1996. Status of pacific salmon and steelhead escapements in southeastern Alaska. Fisheries (Bethesda), **21**: 6–18.

Bilby, R.E., Fransen, B.R., and Bisson, P.A. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. Can. J. Fish. Aquat. Sci. **53**: 164–173.

Borchardt, M.A. 1996. Nutrients. *In* Algal ecology. *Edited by* R.J. Stevenson, M.L. Bothwell, and R.L. Lowe. Academic Press, San Diego, Calif. pp. 183–227.

Chapman, D.W. 1966. Food and space as regulators of salmonid populations in streams. Am. Nat. **100**: 345–357.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. **54**: 187–211.

Johnston, N.T., Perrin, C.J., Slaney, P.A., and Ward, B.R. 1990. Increased juvenile salmonid growth by whole-river fertilization. Can. J. Fish. Aquat. Sci. **47**: 862–872.

Johnston, N.T., Macdonald, J.S., Hall, K.J., and Tschaplinski, P.J. 1997. A preliminary study of the role of sockeye salmon (*Oncorhynchus nerka*) carcasses as carbon and nitrogen sources for benthic insects and fishes in the "early Stuart" stock spawning streams, 1050 km from the ocean. Fish. Project Rep. No. RD55. British Columbia Ministry of Environment, Lands and Parks, Victoria, B.C.

Kline, T.C., Jr., Goering, J.J., and Piorkowski, R.J. 1997. The effect of salmon carcasses on Alaskan freshwaters. *In* Freshwaters of Alaska: ecological syntheses. *Edited by* A.M. Milner and M.W. Oswood. Springer-Verlag, New York. pp. 179–204.

Kyle, G.B., Koenings, J.P., and Edmundson, J.A. 1997. An overview of Alaska lake-rearing salmon enhancement strategy: nutrient enrichment and juvenile stocking. *In* Freshwaters of Alaska: ecological syntheses. *Edited by* A.M. Milner and M.W. Oswood. Springer-Verlag, New York. pp. 205–227.

Lamberti, G.A. 1996. The role of periphyton in benthic food webs. *In* Algal ecology. *Edited by* R.J. Stevenson, M.L. Bothwell, and R.L. Lowe. Academic Press, San Diego, Calif. pp. 533–572.

Levy, S. 1997. Pacific salmon bring it all back home. BioScience, **47**: 657–660.

Mathisen, O.A., Parker, P.L., Goering, J.J., Kline, T.C., Poe, P.H., and Scalan, R.S. 1988. Recycling of marine elements transported into freshwater systems by anadromous salmon. Verh. Int. Ver. Limnol. **23**: 2249–2258.

McCurdy, S., and Bryant, M.D. 1997. The Margaret Lake monitoring program: assessment of the resident cutthroat trout, Dolly Varden, and anadromous salmonids. Progress Report for 1996. USDA Forest Service, PNW Research Station, Juneau, Alaska.

Merritt, R.W, and Cummins, K.W. (*Editors*). 1996. An introduction to the aquatic insects of North America. Kendall/Hunt, Dubuque, Iowa.

Michael, J.H., Jr. 1995. Enhancement effects of spawning pink salmon on stream rearing juvenile coho salmon: managing one resource to benefit another. Northwest Sci. **69**: 228–233.

Minakawa, N. 1997. The dynamics of aquatic insect communities associated with salmon spawning. Ph.D. dissertation, University of Washington, Seattle, Wash.

Mundie, J.H., Simpson, K.S., and Perrin, C.J. 1991. Responses of stream periphyton and benthic insects to increases in dissolved inorganic phosphorus in a mesocosm. Can. J. Fish. Aquat. Sci. **48**: 2061–2072.

Nehlsen, W., Williams, J.E., and Lichatowich, J.A. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. Fisheries (Bethesda), **16**: 4–21.

Parmenter, R.R., and Lamarra, V.A. 1991. Nutrient cycling in a freshwater marsh: the decomposition of fish and waterfowl carrion. Limnol. Oceanogr. **36**: 976–987.

Perrin, C.J., Bothwell, M.L., and Slaney, P.A. 1987. Experimental enrichment of a coastal stream in British Columbia: effects of organic and inorganic additions on autotrophic periphyton production. Can. J. Fish. Aquat. Sci. **44**: 1247–1256.

Peterson, B.J., Deegan, L., Helfrich, J., Hobbie, J.E., Hullar, M., Moller, B., Ford, T.E., Hershey, A., Hiltner, A., Kipphut, G., Lock, M.A., Fiebig, D.M., McKinley, V., Miller, M.C., Vestal, J.R., Ventullo, R., and Volk, G. 1993. Biological responses of an arctic river to fertilization. Ecology, **74**: 653–672.

SAS Institute Inc. 1989. SAS/STAT user's guide, version 6, edition 4. Vol. 2. SAS Institute Inc., Cary, N.C.

Schuldt, J.A., and Hershey, A.E. 1995. Effect of salmon carcass decomposition on Lake Superior tributary streams. J. North Am. Benthol. Soc. **14**: 259–268.

Slaney, T.L., Hyatt, K.D., Northcote, T.G., and Fielden, R.J. 1996. Status of anadromous salmon and trout in British Columbia and Yukon. Fisheries (Bethesda), **21**: 20–35.

Sobczak, W.V. 1996. Epilithic bacterial responses to variations in algal biomass and labile dissolved organic carbon during biofilm colonization. J. North Am. Benthol. Soc. **15**: 143–154.

Steinman, A.D., and Lamberti, G.A. 1996. Biomass and pigments of benthic algae. *In* Methods in stream ecology. *Edited by* F.R. Hauer and G.A. Lamberti. Academic Press, San Diego, Calif. pp. 295–313.

Stockner, J.G., and MacIsaac, E.A. 1996. British Columbia lake enrichment programme: two decades of habitat enhancement for sockeye salmon. Regul. Rivers Res. Manage. **12**: 547–561.

Stockner, J.G., and Shortreed, K.R.S. 1978. Enhancement of autotrophic production by nutrient addition in a coastal rainforest stream on Vancouver Island. J. Fish. Res. Board Can. **35**: 28–34.

Warren, C.E., Wales, J.H., Davis, G.E., and Doudoroff, P. 1964. Trout production in an experimental stream enriched with sucrose. J. Wildl. Manage. **28**: 617–660.

Wheeler, A., and Sutcliffe, D. (*Editors*) 1990. The Biology and Ecology of Rare Fish: the Fisheries Society of the British Isle's Symposium. J. Fish Biol. **37**(Suppl. A).

Willson, M.F., and Halupka, K.C. 1995. Anadromous fish as keystone species in vertebrate communities. Conserv. Biol. **9**: 489–497.

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Concentrations of trace elements in recent and preindustrial sediments from Norwegian and Russian Arctic lakes

Sigurd Rognerud, Trond Skotvold, Eirik Fjeld, Stephen A. Norton, and Anders Hobæk

Abstract: Cu, Hg, Ni, Pb, Se, and Zn concentrations in surface and preindustrial freshwater sediments from 66 lakes in the Norwegian and Russian Arctic were used for studying modern atmospheric deposition of these elements. Statistical analysis showed that, after adjusting for the effects of scavenging factors in sediments (organic matter, Al, and Fe), there were, in general, significantly higher concentrations of Hg and Pb in surface sediments than preindustrial sediments. The differences decreased with increasing latitude and increasing longitude to the east, and in the lakes from arctic islands of Svalbard and along the the arctic coastline of Russia, only Hg concentrations were elevated in surface sediments. We attribute this pattern to modern anthropogenic atmospheric deposition. There were no such differences or regional gradients for the other trace metals. A multivariate analysis of the sediment data showed that Hg and Se were associated with organic matter, whereas Cu, Ni, and Zn were associated with inorganic matter (Al, Fe). There was a shift in Pb association from inorganic matter in the reference sediment to organic matter in the surface sediment, which we interpret as an historic change in importance of sources (from bedrock-derived to atmospheric deposition).

Résumé : Nous avons utilisé les données recueillies sur les concentrations de Cu, Hg, Ni, Pb, Se et Zn dans les sédiments lacustres de la couche de surface et de la couche pré-industrielle de 66 lacs de la région arctique de Norvège et de Russie pour étudier les retombées atmosphériques de ces éléments. L'analyse statistique a révélé, après un ajustement permettant de tenir compte de l'effet de piégeage dans les sédiments (matière organique, Al et Fe), que les concentrations de Hg et de Pb dans les sédiments de surface sont supérieures dans une mesure significative à celles mesurées dans les sédiments pré-industriels. L'écart a diminué avec l'augmentation de la latitude et de la longitude vers l'est; dans les lacs de l'archipel polaire du Svalbard et sur la côte arctique de la Russie, seules les concentrations de Hg étaient plus élevées dans les sédiments de surface. Nous pensons que cette distribution est due aux retombées atmosphériques anthropiques de l'époque moderne. Pour ce qui est des autres métaux présents à l'état de traces, nous n'avons pas trouvé de différence ou de gradient régional. Une analyse multidimensionnelle des données concernant les sédiments a montré que le Hg et le Se étaient associés à la matière organique, tandis que le Cu, le Ni et le Zn étaient associés à la matière inorganique (Al, Fe). Le Pb, associé à la matière inorganique dans les sédiments de référence, était associé à la matière organique dans les sédiments de surface, un changement que nous attribuons à l'évolution de l'importance des sources (le Pb ayant d'abord été surtout d'origine géologique, puis surtout d'origine atmosphérique).
[Traduit par la Rédaction]

Introduction

Knowledge of the spatial distribution of atmospheric deposition of trace metals in the Arctic has been limited by the scarcity of precipitation monitoring stations. Very few measurements of the chemistry of wet deposition and even fewer of dry deposition have been made. Lake sediments typically have concentrations of metals several orders of magnitude higher than those in overlying waters and appear to contain good temporal records of deposition of some metals (Norton and Kahl 1992; Schindler et al. 1995). However, when using changes in concentrations of metals in sediments as a substitute variable for depositional trends, it is important to recognize that sediment focusing, sediment quality, bioturbation, water quality, and inputs of metals from the catchment all influence concentrations of metals in sediment.

Trace elements may reach remote freshwater sites by long-distance transport in the atmosphere (Gregor and Grummer 1989; Barrie et al. 1992, 1997). Analyses for heavy metals in dated snow and ice cores from Greenland confirm that atmospheric deposition of Cu, Pb, and Zn markedly increased concurrently with the industrial revolution more than 200 years ago, followed by a clear decrease since the mid-1960s (Boutron et al. 1995; Hong et al. 1996). The concentration of Hg in air in the northern hemisphere has increased (Slemr and Langer 1992), and elevated concentrations of Hg occur in high-latitude lakes (Johansson 1985; Rognerud and Fjeld 1993; Lockhart et al. 1995; Lucotte et al. 1995). The lower

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mean temperatures of northern lakes may render them more efficient as sinks for volatile contaminants like Hg than warmer southern lakes (Schindler et al. 1995). The long-term implications of Hg contamination for Arctic ecosystems are ominous; northern people consuming contaminated fish have accumulated Hg to surprisingly high levels (Lockhart 1995). However, Se mediates the toxic effects of Hg (Lockhart 1995) and may interfere with the biomagnification of Hg (Fjeld and Rognerud 1993). We have therefore included Se in our study.

Here we report regional variations and temporal changes in concentrations of metals in sediments after adjusting for differences in sediment quality. Our primary objectives were to (*i*) examine the concentrations of Cu, Hg, Ni, Pb, Se, and Zn in surface (recent) and reference sediments (preindustrial or background) of five regions in the Norwegian–Russian Arctic after adjusting for effects of scavenging factors such as organic matter, Fe, and Al (grain size) and (*ii*) discuss these adjusted differences with respect to distance from sources and other factors influencing deposition and transport of metal to sediments in the Arctic.

Materials and methods

This study is based on data from lakes in northern Norway, 6 lakes in the Svalbard archipelago, 1 lake from Bear Island, and 11 tundra ponds along the northern coast of Siberia (Fig. 1). The lakes have been divided into five regions: Nordland (N), Troms (T), and Finnmark (F) counties in northern Norway; Svalbard (S) region; and the Russian (R) region (Siberian coastline). Emissions from anthropogenic sources in Eurasia contribute more than half of the pollution of the Arctic atmosphere in winter. The major sources include the Urals, the Kola Peninsula, the Norilsk area, and the industrial regions of central Europe (Pacyna 1995). In summer, the emissions from sources in Europe seems to be more important than those from the former Soviet Union (Pacyna and Ottar 1988).

In general the lakes were oligotrophic, slightly acidic to circumneutral (median pH 6.9, range 5.3–7.8), and low in total organic carbon (median TOC 2.0 mg $C \cdot L^{-1}$, range: 0.5–8.7)

Our data set contained observations on 23 variables. The variables represent morphometric and chemical characteristics of the lakes and are likely to affect heavy metal accumulation in sediment.

Lake characteristics and geology

The lakes were located from 5 to 548 m above sea level, with a median value of 95 m. The Siberian ponds were shallow (≈1 m) with small surface areas (<0.6 ha). The other lakes were generally small to medium sized; typically 10–30 m deep with a surface area of 0.2–3 km^2 and catchment areas of 5–50 km^2.

Tree vegetation at lower elevations in northern Norway is dominated by birch (*Betula pubescens* ssp. *tortuosa*) and pine (*Pinus sylvestris*). At higher altitudes and in the Svalbard and Russian regions, trees are absent and tundra vegetation prevails. Geologically, northern Norway is underlain by the northern part of the Precambrian Baltic shield bordered by the Caledonian fold belt to the west. The Precambrian basement is divided into gneisses and supracrustal belts intruded by gabbro, anorthosite, and granite in the northeast. The Caledonides are a series of allochthonous thrust sheets or nappes overthrust to the east. The area has been repeatedly glaciated by continental ice sheets during the Pleistocene. The valleys and areas with moderate relief are covered by till or glaciofluvial gravels and sands. Bedrock is well exposed in the west and at higher elevations (Eden and Bjørklund 1994).

Most of the Russian ponds are located close to the ocean on glaciomarine plains, but some are located on sand banks and spits, developed by recent longshore movement of unconsolidated material from northwest to southeast. The Quaternary deposits are typically deep and consist of glacial and glaciomarine loamy and sandy sediments. A few ponds are located at higher elevation where glacial sediment is absent or very thin. Granites and gneiss (Baltic Shield) occur in the west with different shales and sandstones to the east.

The lakes on Svalbard and the one on Bear Island are located mainly on sedimentary rocks (sandstones, shales, and calcareous rocks of Carboniferous, Triassic, Jurassic, and Cretaceous age) or their metamorphic equivalents. Ice cover on the lakes ranges from about 6 months in northern Norway to 9 months on Svalbard.

Sampling procedures

Sediment samples were collected from the deepest part of each lake during the years 1990–1992. We used a modified Kajak–Brinkhurst (KB) gravity corer (Mudroch and Azcue 1995). Instead of using a messenger to close the valve, a thin membrane covers the end of the corer, which closes automatically when the water flow through the tube stops. This closing mechanism requires the use of a cap on the top of the core tubes wide enough to ensure a unrestricted water flow during the descent of the corer. The 75 cm long core tubes (plastic), with a 6.5 cm inner diameter, were sharpened at the lower end and the tube walls were milled down to ≈2 mm.

Both the deepest part of the lake and the exact depth at the coring site were determined with a portable echosounder. The core sampler was lowered slowly down to 2 m above the sediment surface and even more slowly the last 2 m. It then penetrated the sediment gently by its own weight and was not allowed to tilt or sink too deeply into the sediment. Only cores with apparently undisturbed sediment–water interfaces were used for the study. Disturbance of the core sample is mainly a function of the speed of impact and the surface area of the core (Mudroch and Azcue 1995). The slow entry and penetration of the sharpened, thin-walled coring tube into the sediment is essential to prevent loss of surficial sediments and minimize core shortening or any associated core deformation (Blomqvist 1991). Studies with radioactive tracers in sediments have shown that a KB core sampler (5 cm inner diameter) of the type we used, can capture the upper 30 cm of the sediment while providing unbiased estimates of contaminant inventory in lake sediments (Stephenson et al. 1996). These studies concluded that, when used with care, potential artifacts caused by the hydraulic "bow wave" associated with the lowering of the sampler and progressive thinning of sediment layers entering the device as frictional resistance to coring build up inside the core are not a problem gravity core samples of less than 30 cm.

The cores were extruded and sectioned in the field as soon as possible after their retrieval to minimize disturbance of the flocculant surface sediments. Core sections were placed in acid-washed polyethylene cups, stored in the dark in a cold-storage bag and frozen within 12 h after collection. The subsamples for grain size analysis were not frozen.

To document changes in concentrations of heavy metals in the sediments we analyzed the upper 1-cm surface and a layer from the deepest part of the core, normally from 30 to 40 cm. We define the deepest layer as a "reference layer," likely to have been deposited in preindustrial times and therefore representing the natural background concentrations of metals. The water samples were taken at a depth of 1 m at the same time we collected the cores.

Analytical methods

The pH was measured with an Orion Model 901, equipped with a combination glass–calomel electrode. The total organic carbon (TOC) was measured by photochemical UV and wet oxidation, with an Astro Model 2001.

Dried sediments were analyzed for loss on ignition (LOI) by combusting them at 550°C for 2 h. Sediment was digested in concentrated HNO_3 (0.5–1 g/10 mL) under pressure at 120°C and then diluted with distilled water to a final volume of 100 mL.

Concentrations of Pb, Cu, Zn, Ni, Fe, and Al were analyzed by

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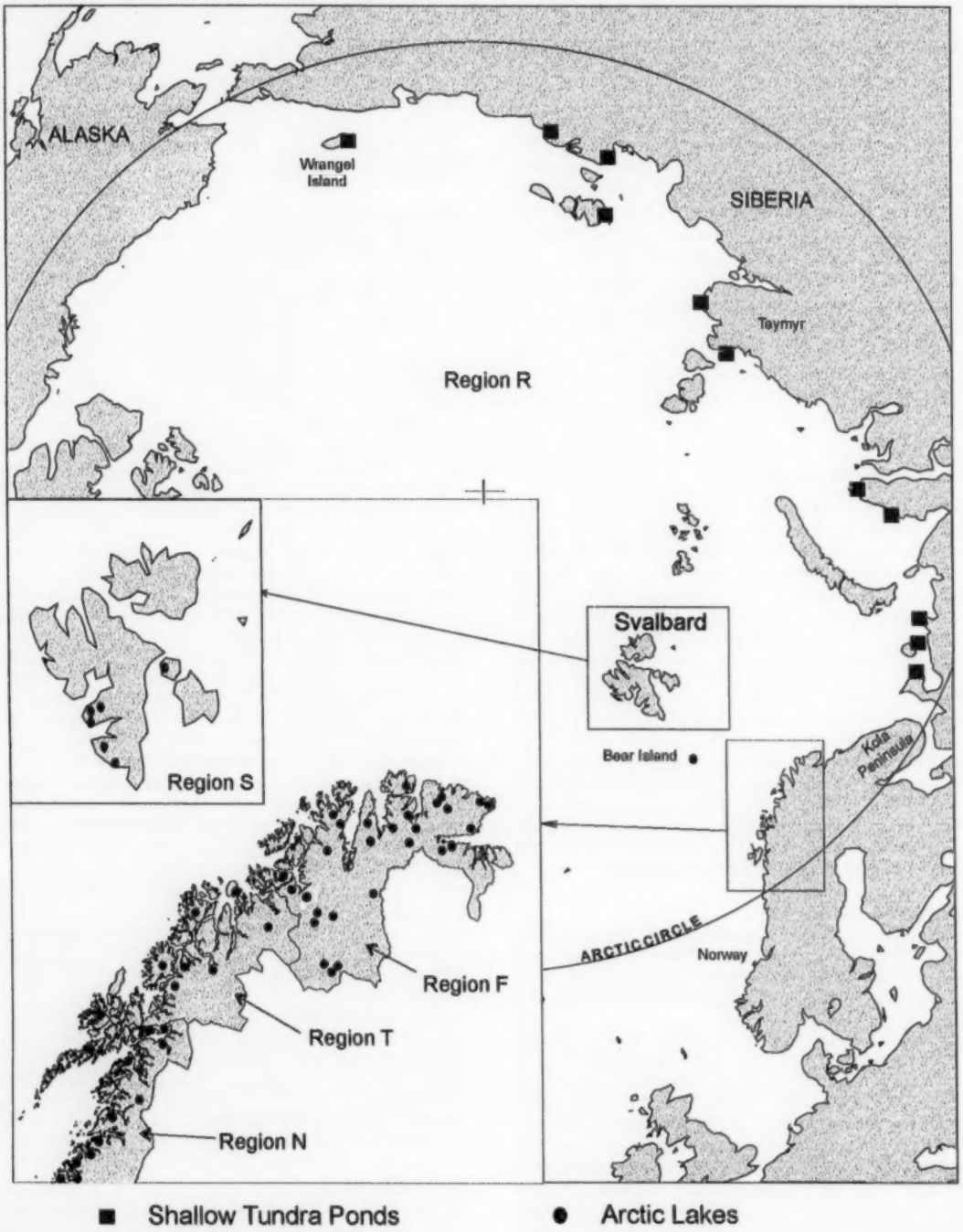
Fig. 1. Location of the 55 lakes (solid circles), 11 Siberian ponds (solid squares), and the different regions.



inductively coupled plasma atomic emission spectrometry (ICP-AES). Detection limits ($\mu g \cdot g^{-1}$, dry weight) were as follows. Pb, 6; Cu, 1; Zn, 1; Ni, 2; Fe, 5; Al, 12. Standard reference sediment BCR-320 from Community Bureau of Reference, Brussels, were submitted randomly among samples before analysis. The analytical results were systematically lower than the certified total values. The bias were usually less than 10% for Fe, Cu, Zn, and Pb; 10–20% for Ni; and 35–45% for Al. The bias is most likely due to an incomplete dissolution of refractory silicates by the nitric acid digestion. The results from the replicate analysis of the reference sediment indicate a

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precision (coefficient of variation) of less than 5% for Pb, Cu, Zn, and Ni and less than 10% for Al and Fe.

Concentrations of Hg and Se were analyzed by instrumental neutron activation analysis (INAA). About 0.3 g air-dried samples were irradiated for 20 h together with standard solutions of Se and Hg. Then the samples were treated with acids (first H_2SO_4, and HNO_3 and later HCl and HBr), and Se and Hg were distilled as chlorides and bromides and precipitated as sulphides. The sulphides were filtered onto membrane filters and measured for induced radioactivity. Irradiated standards were treated in the same way as the samples. After the first measurements, determination of the relative chemical yield in standards and samples is done by reactivation. The relative chemical yields are determined by setting the standard value equal to 1 and comparing the samples with the standards. The first values were then corrected for differences in chemical yields. The absolute chemical yield for Se are usually 85–100%, and 60–80% for Hg.

We use LOI as an indirect measurement of organic carbon within the sediments. Organic carbon constitutes approximately 50% of the LOI. However, adjustments are necessary for sediments with a high Fe content because of the loss of water associated with ferric hydroxides (Fjeld et al. 1994). In general, the sediments in the present study had a low iron content (4–6%), and for practical reasons such adjustments are not necessary.

The sediments of 15 randomly selected lakes from Troms and Finnmark Counties were analyzed for grain size distribution. The samples were split into coarse (≥ 0.063 mm) and fine (pelitic; <0.063 mm) fractions by wet sieving.

Statistical analysis

We transformed most data to improve normality, stabilize variance, and reduce the excessive influence of outliers. Most variables have been logarithmically transformed (base 10), except Se and Zn, which were square-root transformed, and Al, which was untransformed.

We first made an analysis for each of the trace metals and tested for concentration differences between sediment depths (surface sediments vs. reference sediments), regions, and the interaction between sediment depth and region. Our main hypotheses were that the concentrations in the surface sediments were higher than in the reference sediments within regions but that the differences decreased in the more northern regions. We could not analyse the data as an ordinary factorial analysis of variance, because (*i*) the surface and reference sediment were not independent of lakes (we regard them as repeated measures on the same subject), and (*ii*) the sediment concentrations had to be adjusted for effects of influential covariates. By adjusting for the effects of influential covariates, smaller standard errors in the estimated means may be obtained. We used the method of repeated measures of covariance (ANCOVA), allowing for covariates to vary within subjects (lakes). Lakes were treated as a random factor. We used the general linear model procedure in JMP 3.2 (SAS Institute Inc., Cary, N.C.) to do these analyses.

Then, the multivariate relations between the trace elements and the explanatory variables (LOI, Al, and Fe) were visualized by redundance analysis (RDA), where we partialed out the effects of different regions. RDA is a constrained form of (multivariate) multiple regression. It is intermediate between principal component analysis (PCA) and separate multiple regressions for each of the dependent variables. Whereas PCA is an eigenvector extraction technique using only a matrix of input variables (the **Y** matrix), RDA is a constrained form in the sense that the underlying dimensions in the **Y** matrix (latent variables) are forced to be multiple linear regressions of the independent variables (the **Z** matrix). For a detailed treatment on RDA, see Ter Braak and Prentice (1988). The RDA was done with an algorithm from Ter Braak and Prentice (1988), implemented in MATLAB 4.2 (MathWorks, Natick, Mass.).

RDA leads to a biplot diagram that simultaneously displays the main pattern of the dependent variables (the **Y** matrix), as far as this variation can be explained by the independent variables (the **Z** matrix), and the main pattern in correlation coefficients between dependent and independent variables. In the biplot, dependent variables are indicated by points, whereas the independent variables are indicated by arrows. The variables represent different gradients in the data set. Variables (indicated by arrows or points) pointing in roughly the same direction indicate that they are positively correlated; variables crossing at right angles indicate near-zero correlation, and variables pointing in opposite directions indicate high negative correlation. The length of the variables (the arrows or distances from the origin to the points) are proportional to the rate of change in their directions and indicate the importance of the variables in the analysis.

Our strategy for building the ANCOVAs was first to test for effects of sediment depth and regions, after adjusting for the influence of some high-priority covariates (LOI, Al, or Fe in sediments). Then, if necessary, we reestimated the models after excluding covariates with nonsignificant effects, and we also checked for effects of other relevant covariates (pH and TOC of lake water, lake depth, catchment, and lake surface area). Our choices were based on the following rationales.

Many trace elements complex readily with organic ligands and are closely connected to the carbon cycle of lakes (Santschi 1988). Trace elements with high affinity to organic ligands should therefore be associated with the organic fraction of sediments (LOI).

A linear relationship between trace metal concentrations and grain size is common, because of the inverse relationship of the abundance of binding sites (i.e., surface area) and grain size (diameter) (de Groot et al. 1982). Consequently, to compare the metal concentrations in sediments from different areas and to determine changes in the concentration of metals from reference to modern sediment, adjustments have to be made for differences in grain size. The fine-grained fraction in sediments is commonly richer in Al–silicate minerals as well as Al-rich weathering products and Al-rich particulate organic matter. Our lakes have near-neutral pHs and we assume that most of the total Al in sediment is associated with primary Al minerals. There was a strong correlation between Al concentration and grain size distribution (pelite fraction) from a subset of lakes in region F and T ($r = 0.83$, $n = 15$). Therefore, the concentration of Al is used as a surrogate explanatory variable for the pelitic fraction in the statistical analyses.

Organic matter and Fe–Mn oxy-hydroxides coat fine-grained minerals (or may, by themselves, be fine grained); trace metals are very commonly associated with these coatings (Salomons and Förstner 1984). In our lake sediments Mn/Fe ratios are low (0.002–0.03) indicating that Fe probably dominates the grain coatings.

The pH may strongly influence the speciation and the dissolved fraction of many trace elements (Salomons and Förstner 1984), as well as the scavenging effectiveness of particles settling through the water column. Lake depth may influence concentrations of trace metals in sediment because of focusing of organic matter and fine-grained inorganic particles (Håkanson and Jansson 1983).

Results

Generally, there were systematically higher concentrations of Hg and Pb in surface sediments than in reference sediments in all regions, with the largest differences (a factor of two to five) in the southernmost regions (N and T). No such differences were found for the other trace elements (Figs. 2 and 3). However, the surface and reference sediments differed in their composition of important scavenging factors. The organic concentrations (LOI) were generally higher in the surface sediments, particularly in the regions of T and R, where the concentrations were twice as high as in the reference sediments (Table 1). Also, there were generally slightly higher Fe concentrations in surface sediments, except for region R where the mean value was twice as high (Table 1). For Al there were only

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Fig. 2. Unadjusted and adjusted means (with standard errors) of Hg, Pb, and Se concentrations in lake sediments. The adjusted means are least square means from ANCOVAs, adjusted for differences in LOI (Hg, Pb, and Se) and Al (Pb). All estimates are based on transformed data (Hg and Pb, logaritmically; Se, square root). The hatched bars show reference sediments (sediment depth >30 cm), whereas open bars show surface sediments (0–1 cm).

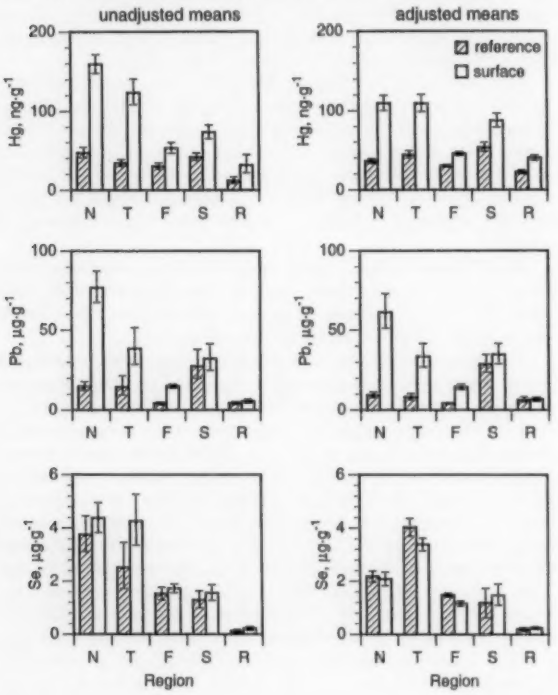
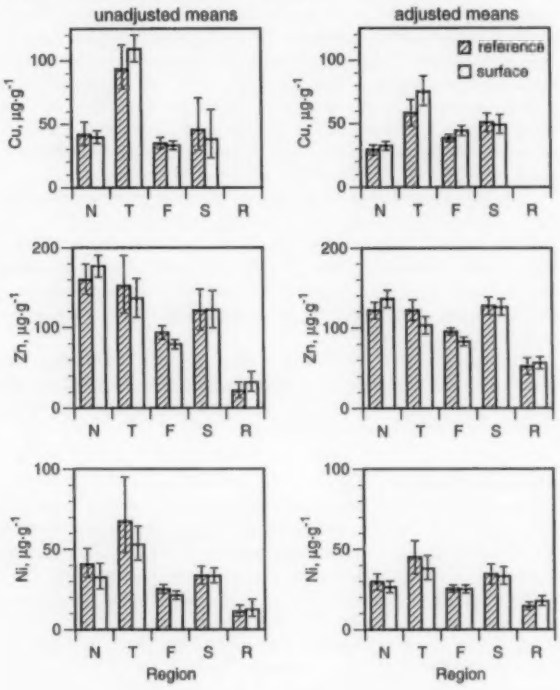


Fig. 3. Unadjusted and adjusted means (with standard errors) of Cu, Zn, and Ni concentrations in lake sediments. The adjusted means are least square means from ANCOVAs, adjusted for differences in Al (Cu, Zn, Ni) and Fe (Zn). All estimates are based on transformed data (Cu and Ni, logaritmically; Zn, square root). The hatched bars show reference sediments (sediment depth >30 cm), whereas open bars show surface sediments (0–1 cm).



small differences between surface and reference sediments (Table 1). In the statistical analysis we attempted to adjusted for differences in these covariates when we tested for differences between surface and reference sediments.

The ANCOVAs

Simple continuous covariates (e.g., pH) have only one parameter. Effects of discrete factors (sediment depth and region) or interactions between continuous variables and discrete factors have a parameter for each anticipated degrees of freedom (n – 1 where n is the number of possible levels within the discrete variable). The parameter estimates for such effects are interpreted as the differences from the average of all values, and they sum to zero. Thus, the parameter estimate for the last level of a discrete factor (or the last interaction between a discrete factor and a continous covariate) is not shown in the tables (Tables 2–4) but may be calculated by subtracting the sum of the other estimates from zero.

The graphical presentation of the results shows the unadjusted and adjusted means of the concentrations in surface and reference sediments within each region (Figs. 2 and 3). The adjusted means are the least square mean estimates from the ANCOVAs. They are the predicted values for each region and sediment depth, adjusted for the effects of the covariates by setting them equal to sample means (geometric means for the log-transformed variables LOI and Fe).

Hg

The ANCOVA of Hg in sediments showed that there were significant effects of sediment depth, region, and their interactions, after adjusting for the influence of LOI as a covariate (Table 2). Al and Fe did not improve the model significantly. The F ratio and the parameter estimate indicated a strong positive effect of LOI. In this analysis we excluded one lake from the region R, because it had anomalously high Hg levels.

The effects of sediment depth indicated generally higher Hg concentrations in surface sediments than in reference sediments. However, this effect was moderated by the interaction of sediment depth and region. The interaction effect was negative for the northern regions Finnmark, Russia, and Svalbard, while it was positive for the more southern regions Troms and Nordland. As a result there were only small differences between surface and reference sediments in the northern regions, whereas there were pronounced differences in the southern regions. However, post hoc tests revealed significant differences between concentrations in surface and reference sediments in all regions.

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Table 1. Mean values with standard errors of loss on ignition (LOI) and Fe and Al concentrations in the sediment samples from the study lakes.

Region[a]	Sediment depth[b]	*n*	LOI (%)	Al (%)	Fe (%)
N	Surface	13	28.3±2.6	2.8±0.2	8.9±0.8
	Reference	13	24.5±2.1	3.1±0.3	6.6±1
T	Surface	7	18.7±4.0	3.2±0.2	6.6±1.1
	Reference	7	8.5±2.1	3.4±0.3	6.4±1
F	Surface	28	17.6±1.1	1.8±0.1	6.1±0.9
	Reference	28	14.6±1.8	2.2±0.1	4.5±0.5
S	Surface	7	8.6±1.1	2.3±0.4	4.7±1.2
	Reference	7	7.3±0.7	2.2±0.4	4.9±1.1
R	Surface	11	21.2±7.2	1.3±0.3	2.9±0.7
	Reference	11	9.6±5.2	1.6±0.3	1.4±0.3

[a]N, Nordland; T, Troms; F, Finnmark; S, Svalbard; R, Russian arctic.
[b]Surface, 0–1 cm; reference, >30 cm.

Table 2. Test for effects of sediment depth, regions, and their interactions on Hg concentrations in lake sediments, after adjusting for the effect of covariates.

	Test of effects			Coefficients		
Effect	df	*F*	*p*	Level	Estimate	SE
Intercept				—	1.203	0.060
log LOI[a]	1	64.43	<0.0001	—	0.465	0.058
z_{sed}[b]	1	38.00	<0.0001	Surface	0.152	0.013
Region[c]	4	8.98	<0.0001	F	–0.137	0.018
				N	0.095	0.029
				R	–0.229	0.030
				S	0.132	0.028
Region × z_{sed}	4	8.79	<0.0001	F, surface	–0.062	0.017
				N, surface	0.088	0.021
				R, surface	–0.024	0.023
				S, surface	–0.046	0.027
Lake (region)	60	5.62	<0.0001	—	—	—

Note: The coefficients refer to the parameter estimates from the statistical model employed (analysis of covariance, repeated measures, lake as a random factor). The analysis was performed on log-transformed Hg concentrations ($n = 65$ lakes).
[a]LOI, Loss on ignition (%).
[b]z_{sed}, Sediment depth; two levels: 0–1 cm (surface) and >30 cm.
[c]Five geographic regions (see Fig. 1).

Pb

The ANCOVA of Pb in sediments showed that there were significant effects of sediment depth, region, and their interactions, after adjusting for the influence of the covariates LOI and Fe (Table 3). However, LOI and Fe also showed significant interactions with sediment depth, which indicates that the effect of these covariates were dependent of sediment depth.

The combined effects of sediment depth, region, and their interactions showed that there generally were higher concentrations in surface sediments than in reference sediments but that these differences decreased in the northernmost regions. Post hoc tests revealed that there were significant differences between surface and reference sediments only in the regions of Nordland, Troms, and Finnmark. Also, the net results of the effects of Al, LOI, and their interactions with sediment depth showed that Pb was associated with Al in reference sediments, whereas it changed to an association with LOI in the surface sediments.

Se

There was no significant effect of sediment depth on the Se concentrations in any of the regions. Region, LOI, and the interaction between LOI and region entered the ANCOVA as explanatory variables (Table 4). Se was positively associated with LOI. After adjusting for LOI, there were generally very low Se concentrations in the Russian ponds, whereas the highest concentrations were in the region of Troms. The interaction between region and LOI was negative for Russia and Svalbard, resulting in a weaker effect of LOI in these most northern regions than in the regions of Norway. Without adjusting for the effect of LOI, an analysis of variance (repeated measures) indicated that the Se concentrations in the surface sediments in general were slightly, but statistically significantly, higher than in the reference sediments ($p = 0.007$).

Cu, Zn, and Ni

These three elements behaved very similarly; thus, we treat them together. There was no significant effect of sediment depth in any of these three ANCOVAs, but the concentrations of both Cu and Zn differed significantly among regions. We have omitted the detailed ANCOVA tables for these three element but present the results from some reduced models that are estimated after omitting the nonsignificant terms. Al was an important covariate for all three elements, which were positively associated with Al. There were weak positive effects (borderline significance) of LOI on Zn. We did not include the Siberian ponds in the statistical analysis of Cu, because Cu was not determined in these sediments. The models were

$$\log \mathrm{Cu} = \mathrm{region} + 0.183(\mathrm{Al}) + \mathrm{lake\ (region)} + 1.217$$
$$R^2 = 0.89,\ F = 8.04,\ \mathrm{df} = 54, 106,\ p < 0.0001$$

The effects of the different regions were as follows: N, –0.158; T, 0.188; F, –0.061; S, 0.031. The term lake (region) is a random factor and is set to zero for general prediction purposes.

$$\mathrm{Zn}^{0.5} = \mathrm{region} + 1.11(\mathrm{Al}) + 2.92\log(\mathrm{Fe}) + \mathrm{lake\ (region)} + 5.81$$
$$R^2 = 0.94,\ F = 16.12,\ \mathrm{df} = 67, 131,\ p < 0.0001$$

The effects of the different regions were as follows: N, 1.59; T, 0.51; F, –0.44; S, 1.09; R, –2.75.

$$\log(\mathrm{Ni}) = 0.164(\mathrm{Al}) + \mathrm{lake} + 1.039$$
$$R^2 = 0.89,\ F = 6.83,\ \mathrm{df} = 71, 131,\ p < 0.0001$$

The term lake is a random factor and is set to zero for general prediction purposes.

The redundancy analysis (RDA)

The results from the RDA are summarized in the biplot (Fig. 4). The effects of different regions were partialled out in the RDA. Region R is not included in the RDA because of the lack of data on Cu from this region. The biplot showed that LOI and Fe formed two distinct, but slightly correlated, gradients. Al formed a third gradient, correlated to the Fe gradient but uncorrelated or slightly negatively correlated to the LOI gradient. The eigenvectors indicated that the first RDA axis accounted for 41% of the variation in the data set, whereas the second RDA axis accounted for 31%. Fe in sediments was the

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Table 3. Test for effects of sediment depth, regions, and their interactions on Pb concentrations in lake sediments, after adjusting for the effect of covariates.

	Test of effects			Coefficients		
Effect	df	*F*	*p*	Level	Estimate	SE
Intercept				—	0.742	0.170
Al[a]	1	5.98	0.018	—	0.131	0.055
log LOI[b]	1	1.32	0.25	—	0.114	0.099
z_{sed}[c]	1	13.73	0.0005	Surface	0.308	0.083
Region[d]	4	13.26	<0.0001	F	–0.270	0.037
				N	0.220	0.062
				R	–0.347	0.076
				S	0.338	0.050
log LOI × z_{sed}	1	3.74	0.06	Surface	0.105	0.055
Al × z_{sed}	1	11.70	0.001	Surface	–0.095	0.028
Region × z_{sed}	4	8.56	<0.0001	F, surface	0.065	0.032
				N, surface	0.199	0.045
				R, surface	–0.198	0.053
				S, surface	–0.164	0.048
Lake (region)	61	2.83	0.0002	—	—	—

Note: The coefficients refer to the parameter estimates from the statistical model employed (analysis of covariance, repeated measures, lake as a random factor). The analysis was performed on log-transformed Pb concentrations ($n = 66$ lakes).

[a]Al, Aluminum concentration (%).

[b]LOI, Loss on ignition (%).

[c]z_{sed}, Sediment depth; two levels: 0–1 cm (surface) and >30 cm.

[d]Five geographic regions (see Fig. 1).

Table 4. Test for effects of sediment depth, regions, and their interactions on Se concentrations in lake sediments, after adjusting for the effect of covariates.

	Test of effects			Coefficients		
Effect	df	*F*	*p*	Level	Estimate	SE
Intercept				—	0.160	0.202
log LOI[a]	1	21.07	<0.0001	—	1.003	0.218
z_{sed}[b]	1	0.73	0.4	—	1.003	0.218
Region[c]	4	4.31	0.004	F	–0.654	0.272
				N	–0.617	0.311
				R	0.158	0.208
				S	1.241	0.723
Region × z_{sed}	4	2.25	0.08	F, surface	–0.053	0.027
				N, surface	–0.001	0.031
				R, surface	0.044	0.035
				S, surface	0.079	0.045
log LOI × region	4	25.68	<0.0001	F, surface	0.536	0.270
				N, surface	0.794	0.277
				R, surface	–0.862	0.228
				S, surface	–1.238	0.817
Lake (region)	61	5.13	<0.0001	—	—	—

Note: The coefficients refer to the parameter estimates from the statistical model employed (analysis of covariance, repeated measures, lake as a random factor). The analysis was performed on square-root transformed Se concentrations ($n = 66$ lakes).

[a]LOI, Loss on ignition (%).

[b]z_{sed}, Sediment depth; two levels: 0–1 cm (surface) and >30 cm.

[c]Five geographic regions (see Fig. 1).

variable with the greatest loading on the first RDA axis, whereas the LOI was the variable with the greatest loading on the second RDA axis.

Among the dependent variables, Hg and Se in both surface and reference sediments formed a coherent group together with Pb in surface sediments. This group was primarily associated with the LOI gradient, although Hg and Pb in surface sediments were located towards the Fe gradient. The Fe and Zn vectors pointed almost exactly in the same direction, which indicated that Zn was closely associated with Fe. Ni in both surface and reference sediments, and Pb in reference sediments, were associated with the Al gradient. Cu in reference and surface sediments was positioned between the Fe and Al gradients, reflecting an association with both elements.

Discussion

We showed that there were significantly higher concentrations of Hg and Pb in surface sediments than in preindustrial sediments, after adjusting for differences in concentrations of organic matter, Al, and Fe. These differences decreased with increasing latitude and from west to east (longitude). No regional trends were found for the other elements. The regional differences for Hg and Pb were in concordance with the general atmospheric deposition pattern, which can be anticipated from distance to the main anthropogenic sources and prevailing wind directions (Pacyna 1995). However, sedimentation rates may differ significantly between regions, and it is therefore critical to know the time represented by the analyzed sediment layers.

Chronology and natural background levels

Our sediment samples are not dated. However, we wanted to get some indications of the average age of the analyzed sediment layers, because such information is important for the interpretation of our results. The sedimentation rates from four lakes in the subalpine Finnmark region were in the range of 0.2–0.4 mm·year^{-1} (dated with ^{210}Pb; Norton et al. 1992, 1996). The same range occurred in lakes from the alpine region in southern Norway and in lake Arresjøen at Svalbard (Wathne et al. 1995). Lakes in the subalpine region of southern Norway had sedimentation rates in the range of 0.6–0.8 mm·year^{-1} (Wathne et al. 1995). In most of these lakes, sedimentation rate was rather uniform with sediment depth. Thus, at the lower altitudes in northern Norway the upper centimetre of sediment approximately represents the last 10–15 years. In high-altitude lakes from northern Norway or the remote Arctic areas the probable age of this surface section is 25–50 years. The reference sediments have been subsampled from a layer 30–40 cm below the sediment surface and are therefore at least 300 years old, but most are probably considerably older (≈1000 years, assuming a sedimentation rate of 0.2–0.8 mm·year^{-1}). They therefore represent sediments deposited before the onset of the industrial revolution (beginning of 19th century).

The possibility that the reference sediments have been contaminated by depositions of preindustrial anthropogenic atmospheric pollutions cannot be excluded. Renberg et al. (1994) found a small increased flux of lead in lake sediments from southern Sweden 2000 years ago, a more significant deposition peak 1000 years ago, and an accelerated flux during the 19th and particularly the 20th century. These peaks were explained by the extensive production and use of lead in

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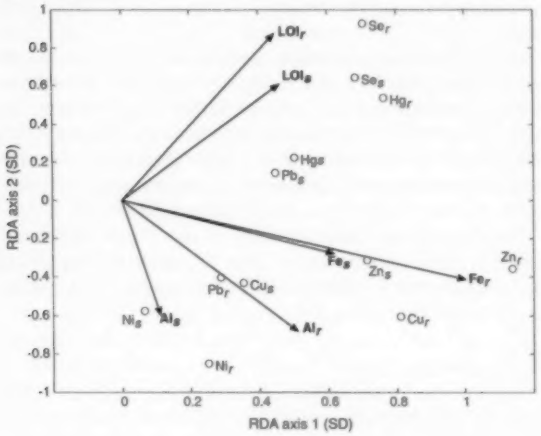
Fig. 4. Biplot based on redundancy analysis of trace metal concentrations in lake sediments (circles) with respect to loss on ignition (LOI) and Al, and Fe concentrations (arrows). Effects of different regions are partialled out. The Siberian ponds are not included in the analysis because of a lack of Cu data. Surface and reference sediments are denoted by the subscripts *s* and *r*, respectively.



Europa starting with the Greek and Roman cultures and ending with the industrial revolution. However, the Arctic regions are far more remote from the preindustrial sources of pollution in Europa, and dated sediments from Svalbard do not show significant systematic changes in metal flux before the industrial revolution (Wathne et al. 1995). Therefore, its resonable to conclude that the trace metal concentrations in our reference sediments are close to natural or background levels.

Hg

The statistical analyses (ANCOVA and RDA) emphasize the importance of organic matter (LOI) as an important covariate for the Hg concentrations. The least square means of the ANCOVA predict significantly higher concentrations in surface sediments in all regions after adjusting for organic matter (expressed as LOI). The association between Hg and organic matter is also demonstrated in the biplot from the RDA, where Hg in both sediment layers were located near the LOI gradient but drawn somewhat towards the Fe gradient. Hg is a trace element with high affinity for organic ligands and, therefore, is associated with the organic fraction of sediments (Santschi 1988). Also, it seems reasonable to assume that the week association to Fe (as seen in the biplot) reflects the coprecipitation of organic colloids and Fe-hydroxides (Salomons and Förstner 1984).

The surface concentrations and the differences from reference values were highest in the Nordland and Troms regions, decreasing towards the Svalbard, Finnmark, and Russia regions. As there were systematically higher concentrations of LOI in surface sediments than in reference sediments, we would have overestimated the anthropogenic contribution to sediment concentrations by using unadjusted values.

The observed regional pattern in northern Norway is consistent with a decreasing south–north atmospheric deposition of Hg for the Nordic countries (Iverfeldt 1991). There are few reliable data on atmospheric deposition of trace elements at higher latitudes in the Norwegian–Russian Arctic. However, our data strongly suggest significant deposition of anthropogenic Hg even in Svalbard and along the northern Siberian coast. Hg in ambient air exists primarily as gaseous Hg^0, and the estimated residence time in the atmosphere is ≈1 year (Slemr and Langer 1991). This allows Hg to be widely circulated in the atmosphere. The oxidation of Hg^0 to Hg^{2+} makes it more suitable for deposition (Iverfeldt 1991). Meteorological conditions in the Arctic do not generally favor the deposition of metals, particularly during winter when dynamic stability in air is strong, preventing vertical mixing (Pacyna 1995). However, for volatile elements like Hg^0, a "cold condensation hypothesis" has been suggested whereby volatile pollutants are emitted in warmer regions and condensed from the atmosphere in cooler environments (Mackay et al. 1995).

A high proportion of the input of contaminants to a lake may be from the catchment. Lake sediments may not correctly record changes in atmospheric deposition of metals because of the time lag caused by watershed retention and release (Schindler et al. 1995). Thus, the catchment may act as a temporary repository for deposited trace elements and then leak substantial amounts of pollutants years after the deposition has decreased. Atmospherically deposited elements like Hg are normally associated with DOC originating in the catchments (Lee and Hultberg 1990; Johansson and Iverfeldt 1994). In a national survey of lake sediments in Norway, Fjeld et al. (1994) observed that LOI in the sediments could be predicted from the TOC and pH of the lake water. Our study lakes are circumneutral. Consequently, LOI for the sediments can be used as a surrogate variable for the supply of humic matter from the catchments. In our statistical analyses we have adjusted for differences in LOI, but the delay in time between atmospheric deposition and response in sediments is not known. It is possible that, at Arctic sites, elements like Hg are deposited in the snowpack over the winter, when the Arctic air is most polluted (Pacyna 1995), and flushed into the lakes during melting over a partly frozen ground as observed by Gregor and Dahl (1990). If so, the time lag between deposition and response in sediments may be shorter than in temperate regions. We estimate, based on ^{210}Pb dating from other arctic lakes, that our surface samples (0–1 cm) were deposited over the last 10–50 years. Thus, the Hg concentrations of surface sediments are influenced primarily by deposition mainly after the 1950s.

Pb

After adjusting for the effects of LOI and Al, the least square means of the ANCOVA predict significantly higher Pb concentrations in surface sediments in three regions on the Norwegian mainland. In contrast to Hg we could not find any significant differences in the two northernmost regions. Thus, the surface concentrations and the increments above reference values decline from south to north. This pattern is consistent with other studies south of the Arctic region (Rognerud and Fjeld 1993; Lucotte et al. 1995) and reflects the anthropogenic impact on the deposition trends. Without adjusting for differences in LOI and Fe, we would have obtained biased estimates of the anthropogenic contributions (differences between surface and reference sediments).

The statistical analyses emphasize the importance of

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organic matter (LOI) and Al as important covariates for the Pb concentrations. In the ANCOVA there was a pronounced shift in the importance of these covariates upcore: Pb in reference sediments was associated with Al, whereas Pb in surface sediments was associated with organic matter. The same pattern was observed in the biplot from the RDA. Naturally occurring Pb in uncontaminated sediments is commonly associated with the fine-grained Al–silicate particles (Loring 1976), but the change in association from Al to organic matter strongly indicate that atmospherically deposited anthropogenic Pb has a high affinity for particulate organic matter in surface waters.

Atmospheric deposition directly on lake surfaces is normally the main part of the total deposition of Pb to lake sediment (Dillon and Evans 1982, Borg and Johansson 1989). Further, Pb has a short residence time in lake water (Borg 1995). Consequently, there is a good correlation between historical data on Pb emissions and changes in Pb concentrations in dated lake sediments (Eisenreich et al. 1986; Norton and Kahl 1992; Renberg et al. 1994). We are confident that our surface sediments contain Pb mainly deposited from the atmosphere during the last 25–50 years at high-altitude lakes in northern Norway or in the remote areas in the Arctic. In lakes at lower altitudes in northern Norway the Pb in our surface sediments has mainly been deposited during the last 10–15 years.

Pb and Hg act as a coherent group with a high correlation in surface sediments (both associated with organic matter). This correlation reflects the same main anthropogenic source areas and distribution patterns in the atmosphere. However, in reference sediments Pb was associated with Al whereas Hg was associated with organic matter. This indicates that Hg in sediments in preindustrial periods was significantly influenced by natural atmospheric sources.

Se

After adjusting for the effects of LOI, the least square means of the ANCOVA predict no significant differences in Se concentrations between surface and reference sediments in any regions. Without such adjustments we would have suspected that, in general, there were elevated concentrations in the surface sediments. The absence of significant differences indicates that Se concentrations in the Arctic atmosphere in the last decades are dominated by natural sources as in preindustrial times. The anthropogenic emissions of Se are primarily from coal and oil combustion and nonferrous metal production (especially Cu and Ni). Deposition of Se in the United Kingdom was heavily influenced by geographical proximity to an emission source, with highest values associated with industrial and coastal zones (Haygarth 1994). The lack of detectable anthropogenic deposition of Se in our lakes is probably due to their remoteness from the large anthropogenic emissions in continental Europe and the United Kingdom.

The ANCOVA predicts decreasing Se concentrations in sediments from the coastal lakes in northern Norway to lakes in Svalbard and especially the Siberian ponds. The interactions between LOI and region identifies a decreasing association between LOI and Se towards the most northern regions, which may indicate a decreasing natural flux of Se in atmospheric deposition. The main part of the total annual flux of Se to the troposphere in the Arctic is natural in origin (Pacyna et al. 1995), and the major natural source are volatile organic selenium compounds of marine origin, such as dimethylselenide (Mosher and Duce 1987; Haygarth 1994). Volatilization rates of gaseous Se species are positively correlated with temperature (Frankenberger and Karlson 1994). Lower ocean temperatures and longer periods with sea ice may be important factors causing reduced emissions of Se from the marine biosphere northeastward. We suggest that this is the major factor explaining the spatial pattern in Se concentrations in lake sediment.

In the biplot from the RDA, Se is closely associated to the LOI gradient. This reflects a strong correlation between Se and LOI in sediments and is consistent with the observations that Se is mainly associated with hydrophobic fulvates in forest soils. These fulvates are more important than mineral weathering in determining the Se content of moor layers in Scandinavian podsols (Gustafsson and Johansson 1992).

The elevated Se concentrations in the Troms region are probably due to anomalies in three lakes (of seven). These lakes are influenced by bedrock that contains elevated concentrations of Se (Neumann 1985).

Cu, Ni, and Zn

After adjusting for the effects of Al (Cu, Zn, and Ni) and Fe (Zn), the least square means of the ANCOVAs predict no significant differences in Cu, Zn, and Ni concentrations between surface and reference sediments in any of the regions. Thus, we have no indication of recent contamination of these elements. The dominating pathway of Zn and Cu input to Scandinavian forest lakes are runoff from the catchments, and the stores of these elements in soil are in excess compared with the flux through the terrestrial compartment (Borg and Johansson 1989). Therefore, the concentrations of these elements are totally dominated by natural sources originating in the catchments.

In the biplot from the RDA these three elements were distributed mainly along the Fe and Al gradients. Ni were located closely to the Al gradient, with slighly negative loadings (perpendicular projection points) on the LOI gradients. This reflects the association of Ni with a fine-grained (Al-rich) mineralogenic fraction of the sediment (Fjeld et al. 1994; Larsen et al. 1996). Cu was placed between the Al and Fe gradients with high loadings on both gradients, which reflects its association with the fine-grained (Al-rich) sediment fraction and complexing iron hydroxides (Salomons and Förstner 1984). Zn was located close to the Fe gradients and loaded strongly on this. However, Zn also loaded strongly on the Al gradients and, somewhat weaker, on the LOI gradients. This reflects an association with the fine-grained sediment fraction and the important roles played by complexing iron hydroxides (summarized by Shuman 1980) and organic matter (Garrett and Hornbrook 1976) in controlling Zn concentrations.

On a global basis the burning of fossil fuels and Ni smelting are the dominant source of atmospheric Ni, while mining and smelting of base metals are the principal sources of airborne Cu and Zn (Pacyna et al. 1995). The largest point sources in the Norwegian–Russian Arctic are smelters located at the Kola Peninsula and in the Norilsk area. Ni and Cu dominate atmospheric metal deposition locally around the smelters located in the western part of the Kola Peninsula, although elevated concentrations of Co, Pb, and Zn occur in precipitation (Sivertsen et al.1992). Cores dated with ^{210}Pb from the region around

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these smelters confirm the importance of these sources since the startup in 1932, and the highest concentrations of Co, Cu, Ni, and Pb occur in the youngest sediments (Norton et al. 1992, 1996). Regional studies on lake sediments indicate that the airborne metals are mainly transported to the northeast towards the Barents Sea, and the deposition declines rather abruptly with distance from the sources (Rognerud et al. 1993; Norton et al. 1996). This is consistent with the observation that metals are associated with the coarse fraction of air particles, the abundance of which declines nearly exponentially from the smelters (Sivertsen et al. 1992). This is the probable reason why we did not detect significant effects of these large point sources in our regional data. Additionally, the concentrations of these elements are rather high in bedrock and soil; therefore, sediments are unsuitable for detecting very low deposition rates of these elements.

Regional patterns

We have compared our results with those from other recent arctic surveys. In our study, we found that, in general, the concentration of Hg and Pb in sediments in the different regions had increased by a factor of 1.6–2.8 and 1–6, respectively, since preindustrial times. These factors are based on the adjusted means from the ANCOVAs. The highest values were found in the southernmost regions. For the other trace elements (Se, Zn, Cu, and Ni) there were no significant increases in the average concentrations. These results are in accordance with other studies from Fennoscandia. The average enrichment factors in lake sediments from northern Sweden were about 2 for Hg, Pb, and Cd, and close to 1 for Zn and Cu (Johansson et al. 1995). In northern Finland (Lapland) the ratio between concentrations in modern and preindustrial sediments were 5–10 for Pb, about 2 for Hg and Cd, less than 2 for Zn and Cu, whereas it varied between 1 and 5 for Ni because of local pollution from a smelter (Mannio et al. 1997).

Low concentrations (0.02–0.06 $\mu g \cdot g^{-1}$, dry weight) of Hg have been found in surface lake sediments from four locations in southern and eastern Greenland, but there were no data on preindustrial sediments (Riget at al. 1997). These concentrations are in the same range as those we found in the Finmark region (northern Norway) and along the Siberian coastline.

In a recent review, Jackson (1997) suggested that northwestern sites in North America are frequently exposed to relatively clean air from the Pacific Ocean and Alaska, whereas the central and eastern sites are often exposed to more heavily contaminated air from the urban and industrial areas in the central and eastern regions of North America. Sediments from four Arctic lakes in northern Alaska did not show significant differences between concentrations in modern and preindustrial sediments for Hg, Cu, Cd, Pb, Zn, and Ni (Allen-Gil et al. 1997). However, Engstrom and Swain (1997) showed that Hg accumulation in three southeastern Alaskan coastal lakes increased by a factor of 1.8–2.1 since preindustrial times. Cores from a lake in the Mackenzie Delta indicate that deposition of Hg, Cd, and Pb has not increased noticeably over the past several decades (Barrie et al. 1997). However, sediment records in seven lakes from Yukon and Northwest Territories in northern Canada, showed ratios of concentrations in modern to preindustrial sediments (or fluxes) in the order of 1.1–7 for Hg and 1.1–10 for Pb (Lockhart et al. 1995; Barrie et al. 1997). Lucotte et al. (1995) studied 10 lakes in northern Quebec (Canada) and found an average flux rate of Hg (adjusted for organic carbon) in modern sediments to be 2.3 times the preindustrial levels. Significant surface sediment flux enrichment was found for Hg and Pb (3.5 and 3.2) in a lake located on Belcher Islands in southern Hudson Bay (Canada), but low enrichments (1.6–1.8) for Cd, Zn, and Cu (Hermanson 1993).

To conclude, our study shows that, in Arctic areas where reliable regional data on anthropogenic atmospheric depositions are difficult to obtain, freshwater sediments can be used as a surrogate medium for detecting mean changes over the last few decades. For interpreting sediment data we emphasize the importance of adjusting for variation in natural environmental factors that influence sediment chemistry. Our data indicate that atmospherically deposited elements such as Hg, Se, and Pb were closely connected to the carbon cycle of the lakes, whereas elements dominated by natural processes in the catchments (Cu, Ni, and Zn) were more associated with geologically derived sediment characteristics (grain size, Fe). We also confirm widespread atmospheric contamination of Hg and Pb at Arctic latitudes. Our results also suggest that marine aerosols are an important source of Se to lakes especially in coastal areas. The atmospheric emissions of the large Cu–Ni smelters in the Russian Arctic affected lakes locally around the smelters. However, no regional effects were detected probably because sediments are unsuitable for detecting low depositions of these elements.

Acknowledgments

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References

Allen-Gil, S.M., Gubala, C.P., Landers, D.H., Lasorsa, B.K., Crecelius, E.A., and Curtis, L.R. 1997. Heavy metal accumulation in sediment and freshwater fish in U.S. Arctic lakes. Environ. Toxicol. Chem. **16**: 733–741.

Barrie, L.A., Gregor, D., Hargrave, B., Lake, R., Muir, D., Shearer, R., Tracey, B., and Bidleman, T. 1992. Arctic contaminants: sources, occurrence and pathways. Sci. Total Environ. **122**: 1–74.

Barrie, L., Macdonald, R., Bidleman, T., Diamond, M., Gregor, D., Smekin, R., Strachan, W., Alaee, M., Backus, S., Bewers, M., Gobeil, C., Halsall, C., Hoff, J., Li, A., Lochkart, L., Mackay, D., Muir, D., Pudykiewicz, J., Reimer, K., Smith, J., Stern, G., Schroeder, W., Wagemann, R., Wania, F., and Yunker, M. 1997. Sources, occurence and pathways. *In* Canadian Arctic contaminants assessment report. *Edited by* J. Jensen, K. Adare, and R. Shearer. Indian and Northern Affairs Canada, Ottawa, Ont. pp. 35–182.

Blomqvist, S. 1991. Quantitative sampling of soft-bottom sediments: problems and solutions. Mar. Ecol. Prog. Ser. **72**: 295–304.

Borg, H. 1995. Trace elements in lakes. *In* Trace elements in natural waters. *Edited by* B. Salbu and E. Steinnes. CRC Press, Inc., London. pp. 177–201

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Borg, H., and Johansson, K. 1989. Metal fluxes to Swedish forest lakes. Water Air Soil Pollut. 47: 427–441.

Boutron, C.F., Candelone, J.P., and Hong, S. 1995. Greenland snow and ice cores: unique archives of large-scale pollution of the troposphere of the Northern Hemisphere by lead and other heavy metals. Sci. Total Environ. **160/161**: 233–241.

de Groot, A.J., Zschuppe, K.H., and Salomons, W. 1982. Standardization of methods of analysis for heavy metals in sediments. Hydrobiologia, **92**: 689–695.

Dillon, P.J., and Evans, R.D. 1982. Whole lake lead burdens in sediments of lakes in southern Ontario, Canada. Hydrobiologia, **91**: 121–130.

Eden, P., and Bjørklund, A. 1994. Ultra-low density sampling of overbank sediment in Fennoscandia. J. Geochem. Explor. **51**: 265–289.

Eisenreich, S.J., Metzer, N.A., Urban, N.R., and Robbin, J.A. 1986. Response of atmospheric lead to decreased use of lead in gasoline. Environ. Sci. Technol. **20**: 171–174.

Engstrom, D.R., and Swain, E.B. 1997. Recent declines in atmospheric mercury in the upper midwest. Environ. Sci. Technol. **31**: 960–967.

Fjeld, E., and Rognerud, S. 1993. Use of path analysis to investigate mercury accumulation in brown trout (*Salmo trutta*) in Norway and the influence of environmental factors. Can. J. Fish. Aquat. Sci. **50**: 1158–1167.

Fjeld, E., Rognerud S., and Steinnes, E. 1994. Influence of environmental factors on heavy metal concentration in lake sediments in southern Norway indicated by path analysis. Can. J. Fish. Aquat. Sci. **51**: 1708–1720.

Frankenberger, W.T., Jr., and Karlson, U. 1994. Microbial volatilization of selenium from soil and sediments. *In* Selenium in the environment. *Edited by* W.T. Frankenberger, Jr., and S. Benson. Marcel Dekker, Inc., New York. pp. 369–387.

Garret, R.G., and Hornbrook, E.H.W. 1976. The relationship between zinc and organic content in center-lake bottom sediments. J. Geochem. Explor. **5**: 31–38.

Gregor, D.J., and Dahl, M. 1990. Final Report on the 1989/1990 Lake Hazen water quality study. Fisheries and Oceans Canada, National Water Research Institute, Burlington, Ont.

Gregor, D.J., and Grummer, W.D. 1989. Evidence of atmospheric transport and deposition of organochlorine pesticides and polychlorinated biphenyls in Canadian Arctic snow. Environ. Sci. Technol. **23**: 561–565.

Gustafsson, J.P., and Johansson, L. 1992. Selenium retention in the organic matter of Swedish forest soils. J. Soil Sci. **43**: 461–472.

Håkanson, L., and Jansson, M. 1983. Principles of lake sedimentology. Springer-Verlag, Berlin.

Haygarth, P.M. 1994. Global importance and global cycling of selenium. *In* Selenium in the environment. *Edited by* W.T. Frankenberger, Jr., and S. Benson. Marcel Dekker, Inc., New York. pp. 1–27.

Hermanson, M.H. 1993. Historical accumulation of atmospherically derived pollutant trace metals in the Arctic as measured in dated sediment cores. Water Sci. Technol. **28**: 33–41.

Hong, S., Candelone, J.-P., Patterson, C.C., and Boutron, C.F. 1996. History of ancient copper smelting pollution during Roman and Medieval times recorded in Greenland ice. Science (Washington, D.C.), **272**: 246–249.

Iverfeldt, Å. 1991. Occurrence and turnover of atmospheric mercury over the Nordic countries. Water Air Soil Pollut. **56**: 251–265.

Jackson, T.A. 1997. Long-range atmospheric transport of mercury to ecosystems, and the importance of anthropogenic emissions—a critical review and evaluation of the published evidence. Environ. Rev. **5**: 99–120.

Johansson, K. 1985. Mercury in sediment in Swedish forest lakes. Verh. Int. Ver. Theor. Angew. Limnol. No. 22. pp. 2359–2363.

Johansson, K., and Iverfeldt, Å. 1994. The relation between mercury content in soil and the transport of mercury from small catchments in Sweden. *In* Mercury pollution. Integration and synthesis. *Edited by* C.J. Watras and J.W. Huckabee. Lewis Publishers, Boca Raton, Fla. pp. 323–328.

Johansson, K., Anderson, A., and Andersson, T. 1995. Regional accumulation pattern of heavy metals in lake sediments and forest soils in Sweden. Sci. Total Environ. **160/161**: 373–380.

Larsen, J., Boyle, J.F., and Birks, J.B. 1996. Variation in the geochemistry of recent lake sediments along a west–east pollution gradient in the Bergen area, Norway. Water Air Soil Pollut. **88**: 47–81.

Lee, V.H., and Hultberg, H. 1990. Methylmercury in some Swedish surface waters. Environ. Toxicol. Chem. **9**: 833–841.

Lockhart, W.L. 1995. Implications of chemical contaminants for aquatic animals in the Canadian Arctic: some review comments. Sci Total Environ. **160/161**: 631–641.

Lockhart, W.L., Wilkinson, P., Billeck, B.N., Hunt, R.V., Wagemann, R., and Brunskill, G.J. 1995. Current and historical inputs of mercury to high-latitude lakes in Canada and to Hudson Bay. Water Air Soil Pollut. **80**: 603–610.

Loring, D.H. 1976. The distribution and partition of zinc, copper, and lead in the sediments of the Saguenay fjord. Can. J. Earth Sci. **13**: 960–971.

Lucotte, M., Mucci, A., Hillaire-Marcel, C., Pichet, P., and Grondin, A. 1995. Anthropogenic mercury enrichment in remote lakes of northern Quebec (Canada). Water Air Soil Pollut. **80**: 467–476.

Mackay, D., Wania, F., and Schroeder, W. H. 1995. Prospects for modeling the behavior and fate of mercury, globally and in aquatic systems. Water Air Soil Pollut. **80**: 941–950.

Mannio, J., Porvari, P., Vartiainen, T., Witick, A., Kinnunen, K., and Verta, M. 1997. Lake sediments as indicators of airborne pollution in Lapland. Results from the AMAP programme. *In* Extended Abstracts from the AMAP International Symposium on Environmental Pollution in the Arctic, 1–5 June 1997, Tromsø, Norway. Vol. 1. *Edited by* L.-O. Reiersen. Arctic Monitoring and Assessment Programme, Oslo, Norway. pp. 410–412.

Mosher, B.W., and Duce, R.A. 1987. A global atmospheric selenium budget. J. Geophys. Res. **92**: 13 289 – 13 298.

Neumann, H. 1985. The minerals of Norway. Skr. No. 68. Norwegian Geological Survey, Trondheim.

Norton, S.A., and. Kahl, J.S. 1992. Paleolimnological evidence of metal pollution from atmospheric deposition. *In* The deposition and fate of trace metals in our environment, 8 Oct. 1991, Philadelphia, Pa. *Edited by* E.S. Verry and S.J. Vermette. USDA For. Serv. Gen. Tech. Rep. No. NC-150.

Norton, S.A., Henriksen, A., Appelby, P.G., Ludwig, L.L., Vereault, D.V., and Traaen, T.S. 1992. Trace metal pollution in eastern Finnmark, Norway, as evidenced by studies of lake sediments. Publ. No. 487/92. Norwegian State Pollution Control Authority, Oslo.

Norton, S.A., Appelby, P.G., Dauvalter, V., and Traaen, T.S. 1996. Trace metal pollution in eastern Finnmark, Norway and Kola Peninsula, northwestern Russia, as evidenced by studies of lake sediment. Acid Rain Res. No. 41/96. Norwegian Institute for Water Research, Oslo.

Pacyna, J.M. 1995. The origin of Arctic air pollutants: lessons learned and future research. Sci. Total Environ. **160/161**: 39–53.

Pacyna, J.M., and Ottar, U. 1988. Vertical distribution of aerosols in the Norwegian Arctic. Atmos. Environ. **22**: 2213–2222

Pacyna, J.M., Scholtz, M.T., and Li, Y.-F. 1995. Global budget of trace metal sources. Environ. Rev. **3** : 145–159.

Renberg, I., Persson, M.W., and Emteryd, O. 1994. Pre-industrial atmospheric lead contamination detected in Swedish lake sediments. Nature (London), **368**: 323–326.

Riget, F., Dietz, R., Asmund, G., and Johansen, P. 1997. Heavy metals in the Greenland terrestrial and freshwater environment. Results from the AMAP programme. *In* Extended Abstracts from the

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AMAP International Symposium on Environmental Pollution in the Arctic, 1–5 June 1997, Tromsø, Norway. Vol. 1. *Edited by* L.-O. Reiersen. Arctic Monitoring and Assessment Programme, Oslo, Norway. pp. 375–377.

Rognerud, S., and Fjeld, E. 1993. Regional survey of heavy metals in lake sediments in Norway. Ambio, **22**: 206–212.

Rognerud, S., Norton, S.A., and Dauvalter, V. 1993. Heavy metal pollution in lake sediments in the border areas between Russia and Norway. Publ. No. 522/93. Norwegian Institute of Water Research, Oslo.

Salomons, W., and Förstner, U. 1984. Metals in the hydrocycle. Springer-Verlag, Berlin.

Santschi, P. H. 1988. Factors controlling the biogeochemical cycles if trace elements in fresh and coastal waters as revealed by artificial radioisotopes. Limnol. Oceanogr. **33**: 848–866.

Schindler, D.W., Kidd, K.A., Muir, D.C.G., and Lockhart, W.L. 1995. The effects of ecosystem characteristics on contaminant distribution in northern freshwater lakes. Sci. Total Environ. **160/161**: 1–17.

Shuman, L.M. 1980. Zinc in soils. *In* Zinc in the environment. Part 1: Ecological cycling. *Edited by* J.O. Nriagu. John Wiley & Sons, New York, pp. 39–69.

Sivertsen, B., Makarova, T., Hagen, L.O., and Baklanov, A.A. 1992. Air pollution in the border areas of Norway and Russia. Summary report 1990–1991. Publ. No. 8/92. Norwegian Institute for Air Research, Oslo.

Slemr, F., and Langer, E. 1992. Increase in global atmospheric concentrations of mercury inferred from measurements over the Atlantic Ocean. Nature (London), **355**: 434–437.

Stephenson, M., Klaverkamp, J., Motycka, M., Baron, C., and Schwartz, W. 1996. Coring artifacts and contaminant inventories in lake sediment. J. Paleolimnol. **15**: 99–106.

Ter Braak, C.J.F., and Prentice, I.C. 1988. A theory of gradient analysis. Adv. Ecol. Res. No. 18. pp. 271–317.

Wathne, B.M., Patrick, S.T., Monteith, D., and Barth, H. 1995. AL:PE 1 Report for the period April 1991 – April 1993. Publ. No. EUR 16129. European Commission, Brussels.

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Ecological relationship between freshwater sculpins (genus *Cottus*) and beach-spawning sockeye salmon (*Oncorhynchus nerka*) in Iliamna Lake, Alaska

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Abstract: The interaction between two sculpin species, *Cottus cognatus* and *Cottus aleuticus*, and island beach spawning sockeye salmon (*Oncorhynchus nerka*) was examined in Iliamna Lake, Alaska. We conclude that sculpins actively move to specific spawning beaches and that the initiation of their movements precedes the start of spawning. Sculpin predation on sockeye eggs is positively dependent on sculpin size and on the state of the eggs (fresh versus water hardened), with the largest sculpins able to consume nearly 50 fresh eggs at a single feeding and 130 over a 7-day period. The number of sculpins in sockeye nests is greatest at the beginning of the spawning run, lowest in the middle, and high again at the end, with peak numbers of over 100 sculpins per nest (1 m^2). We discuss the results in terms of energy flow of marine-derived nutrients into an oligotrophic system and in terms of the coevolution of sockeye spawning behavior and the predatory behavior of sculpins.

Résumé : Nous avons étudié les interactions entre les chabots *Cottus cognatus* et *Cottus aleuticus* et le saumon rouge (*Oncorhynchus nerka*) qui fraie près des plages des îles au lac Iliamna, en Alaska. Nous sommes parvenus à la conclusion que les chabots se rendent à certaines plages de fraye, et commencent leur déplacement avant le début de la fraye. Nous avons constaté que l'activité de prédation du chabot, qui se nourrit d'oeufs de saumon rouge, dépend de la taille du chabot et de l'état des oeufs (frais ou durcis), les plus gros chabots pouvant consommer presque 50 oeufs frais en une seule période d'alimentation et 130 oeufs en 7 jours. Les chabots présents dans les nids des saumons sont surtout nombreux au début de la fraye; leur nombre est au plus bas vers le milieu de la période de fraye et redevient élevé vers la fin; en période maximale, on en trouve plus de 100 par nid (1 m^2). Nous analysons nos résultats sous l'angle du transfert d'énergie survenant à la faveur du passage de nutrients d'origine marine à un système oligotrophe ainsi qu'en examinant l'évolution parallèle du comportement de fraye du saumon rouge et de l'activité prédatrice du chabot.
[Traduit par la Rédaction]

Introduction

Pacific salmon (genus *Oncorhynchus*) spawning runs are highly predictable in both space and time (e.g., Wood and Foote 1996). These runs result in the transfer of significant amounts of marine-derived nutrients to unproductive freshwater systems (e.g., Bilby et al. 1996). Temporally and spatially predictable resources are important in animal migrations on both local and broad geographic scales, with salmonids representing the positive extreme in predicability as a food resource for other animals (Willson and Halupka 1995). However, few studies have actually examined in detail the ecological relationship between salmonids and those species that exploit them.

Fish predation on salmon eggs has been noted in many cases, but its effect on salmon production remains questionable. Freshwater sculpins, family Cottidae, have long been suspected as significant predators on salmonid eggs (e.g., Reed 1967; Savino and Henry 1991). However, Moyle (1977) concluded that while sculpins clearly ate salmonid eggs, they tended to eat eggs that were already exposed and at drift, and hence were unlikely to have survived in any case.

Iliamna Lake, Alaska, is the single largest sockeye salmon (*Oncorhynchus nerka*) producing lake in the world, with total runs sometimes in excess of 30 million fish (Eggers and Rogers 1987). Sockeye salmon spawning on island beaches in Iliamna Lake can sometimes account for near 30% of the total escapement to the lake. These beach populations are notable in that the females have a very short spawning duration (e.g., Hendry et al. 1995) and among the largest eggs observed in the species (Quinn et al. 1995).

Iliamna Lake island beaches are typified by large gravel, with large interstitial spaces and few fines (e.g., Leonetti 1997). This high porosity allows wind-generated under-gravel water flow to supply the developing embryos with oxygen, but may also account for the presence of coastrange (*Cottus aleuticus*) and slimy sculpin (*Cottus cognatus*) that have been observed feeding on salmon eggs (Kerns and Donaldson 1968). The greater the substrate size, the greater the ease with which sculpins can move within it, and the more vulnerable salmon eggs are to predation (Phillips and Claire 1966). These sculpins

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derive a significant amount of their nutrients from predation on sockeye eggs and fry (Kline et al. 1993), but questions remain with regard to how sculpin behavior is affected by this resource, how and if sculpins affect this resource, and how and if sockeye salmon behavior is or has (in an evolutionary sense) been affected by the presence of egg predators.

We examine the ecological relationship between the two sculpin species and sockeye salmon spawning on island beaches in Iliamna Lake and compare the distributions of sculpins and spawning sockeye salmon in space and time. We then estimate the magnitude of sculpin predation on the production of sockeye salmon on the beaches through feeding experiments and estimates of numbers of sculpins and sockeye on the beaches. Finally, we address whether "predator satiation", as a means for reducing clutch predation (e.g., Sweeney and Vannote 1982; Furness and Monaghan 1987), may account for the short spawning run and whether sculpin gape limitation may account for the large egg size of island beach sockeye (e.g., Northcote 1954).

Methods

Survey of sculpin and sockeye salmon abundance

In 1992, we established a series of 12 fixed sampling locations (hereafter referred to as locations 1–12) along a 180-m section of beach on Woody Island, Iliamna Lake, Bristol Bay, Alaska. The sampling locations covered an area of the beach from an inner bay where sockeye do not spawn (locations 1–5) through the known spawning area (locations 6–10) to the outer point of the bay (locations 11–12) where, again, sockeye spawning does not occur (see fig. 1 of Quinn and Foote 1994). Locations 6–10 were the only ones where sockeye eggs were found buried in the gravel. Hereafter, we refer to the area spanned by these five locations as the "spawning area" and the other seven locations as the "nonspawning area."

Each of the 12 sampling locations had two sampling sites located on a perpendicular path from shore and centred at 0.75 and 1.5 m water depths (the water level rose 0.5 m throughout the month of study). Within sites, we estimated the density of sockeye females and sculpins, with the area surveyed dependent on the species. Sampling sites for sockeye consisted of 5 × 5 m squares that were delineated at the corners by large marked rocks. Sampling sites for sculpins consisted of a 1-m^2 area in the centre of the 5-m^2 area, delineated by a labelled rock (1–12) and a PVC quadrat carried by the surveyor. The centres of the sampling sites (at a given depth) were spaced about 16.3 m apart, with a distance of about 11.3 m between the edges of adjacent 5-m^2 sampling sites. Perpendicular to the shoreline, the distance between sampling sites within a location varied dependent on the slope of the shoreline, from about 15 m in the inner and outer bay where the slope was gentle to only a few metres in central spawning area where the slope was steeper. Sockeye spawned at greater depths than we were able to sample (to about 3.5 m), but our sampling area included most of the area of spawning activity (Quinn and Foote 1994).

The sites were surveyed by two snorkelers 20 times from 2 August to 7 September (on 2 August, only the 0.75-m sites were surveyed). This period encompassed the total spawning run of sockeye salmon, plus 1 week on either end. All sockeye females holding position within the 5-m^2 grid were counted, including those whose central position was on the imaginary line connecting the corner points. To provide a more specific measure of the temporal nature of egg deposition, each female was identified as to whether she had or had not yet completed spawning (see Quinn and Foote 1994). We refer to these as "spawned out" and "breeding," respectively.

Sculpin numbers were assessed within the same twenty-four 1-m^2 sites over the course of the season to minimize the total area of disturbance. Sculpin numbers were assessed by surface counts and then by digging among the rocks with the use of a steel pole. The gravel was dug to a depth at which no more sculpins were uncovered (10–20 cm). Counted sculpins were gently guided out of the grid. We did not differentiate sculpins by species, but their length was assigned to one of three predetermined categories (small, >50 to <75 mm; medium, >75 to <100; large, >100 mm total length (TL); the PVC quadrat had eight 0- to 10-cm scales marked on it). Fewer than 5% of all sculpins observed were <50 mm TL.

We found no significant differences in either sockeye or sculpin numbers between sites–depths within sampling locations and strong positive correlations between sockeye and sculpin numbers over time within each site (results not presented). As such, we present only the mean number per sampling location, pooled over the two depths.

Length and condition of sculpins

We examined the weight–length relationship of slimy and coastrange sculpins captured by dip net before (3–5 August), during (14 August), and after (30 August) the sockeye spawning period in 1993 to determine if sculpins gain weight in association with the spawning of salmon. We did not use condition factor indices (see Cone 1986), rather, within species, we first compared the natural logarithm of the weight–length relationship over time with analysis of covariance (ANCOVA) and then adjusted the weight of each fish to the natural logarithm of mean total length of both species collected (4.238). The adjustment for each individual was made as follows: $\ln WT_i' = \ln WT_i - (\text{pooled slope}_s \times (\ln TL_i - 4.238))$ where $\ln WT_i'$ is the adjusted weight of the ith fish, $\ln WT_i$ is the weight of the ith fish, and pooled slope_s is the pooled slope from ANCOVA per each species (2.86 and 3.42 for slimy and coastrange sculpins, respectively). Twelve sculpins with large internal parasites were excluded from the analyses.

Feeding studies

In experiments run in an enclosed bay, we examined (*i*) the number of eggs that could be consumed by hungry sculpins of both species and various sizes within a 1-h feeding period and (*ii*) the potential number of eggs that could be consumed over the course of the major sockeye spawning period (7 days). The former provides an estimate of the number of eggs that could be eaten during a single spawning, and the latter provides an estimate of the overall effect of sculpin egg consumption on sockeye production.

Egg consumption in a single feeding period

The diameter and hardness of salmon eggs change once they are exposed to water. Over the course of about an hour, they absorb water and harden in a process referred to as "water hardening". We considered that this process might have substantial effects on the number of eggs that might be consumed by a given sculpin and on the minimum size of sculpin that could consume eggs. Hence, for both sculpin species, we examined egg consumption of both "fresh" eggs and those that had been water hardened for at least 1 h in lake water. We measured the weight of 40 eggs together (± 0.01 g) and the diameter of 10 eggs in a row (± 1 mm) before each trial. The eggs from eight beach-spawning female sockeye were used, with eggs from three females used in both fresh and water-hardened treatments. We examined the relationship between egg consumption and sculpin length in a series of 12 experimental containers. The enclosures, made of fine-mesh stainless steel screen, had 15-cm-high sides mounted on a 40 × 40 cm square bottom. The cages were placed on metal stands, with the water level in each at about 10 cm. The bottom of each cage was covered with fine gravel upon which the eggs were clearly visible. A 15-cm-long, 6-cm-diameter weighted black ABS pipe was provided as shelter for the sculpins.

Sculpins were collected from spawning grounds by snorkelers using dip nets and then held without food for 4 days prior to testing. On the eve of a trial, six sculpins of each species were selected and placed

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singly, and randomly, in each of the enclosures. A trial consisted of placing 40 eggs near each sculpin and then collecting and counting all remaining whole eggs at the end of a 1-h period. To get a more accurate estimate of what we observed in the wild, only sculpins that showed a propensity to feed in our chambers were tested. This propensity was tested by placing a few eggs in a 50-cm-long, 1-cm-diameter glass tube, with a squeeze ball on one end and a screen blocking the other end. The eggs were "moved" in front of the sculpin by lightly squeezing the ball. The sculpins were selected for testing if they attempted to feed on the available eggs. Most sculpins responded, but the proportion was not recorded. In addition, 10 sculpins >70 mm that either did not feed or fed only on one egg during testing were considered outliers and excluded from the analysis.

Egg consumption over a 7-day period

This experiment was conducted in 1993 and 1994. The design was balanced over years in terms of size range and species tested to avoid any confounding effects of time and weather. Water temperature (± 0.1°C) was recorded with a hand-held thermometer about six times per 24-h period in 1993 and with a HOBO™ temperature logger every 8 min in 1994. In 1993, the average water temperature during the experiment was 12.69 ± 0.15°C (SE, $n = 39$) and in 1994 was 13.31 ± 0.05°C ($n = 750$).

Experiments were conducted in opaque floating plastic containers with a removable lid, with the lid just above the lake surface. The containers measured 35 × 28 × 15 cm deep and were divided in half with a fine-mesh vertical stainless steel screen so that two sculpins could be tested simultaneously within each container. Fresh lake water could enter through the containers by 5 × 10 cm rectangular openings covered with fine screen at each end of the container. Each of 12 containers was tethered to separate posts in 1.5 m of water. Weighted black ABS pipes were provided for shelter.

We examined sculpins over 70 mm TL because these were most abundant on the spawning grounds. We tested six sculpins of each species in four size stanzas (70–79, 80–89, 90–99, and >99 mm). In each container, we placed a single sculpin on one side of the divider and a size-matched member of the other species on the other. No interactions between sculpins were observed. For 7 days, we repeated the process when at about noon each day, we gave each sculpin a set number of fresh eggs and then collected all of the remaining eggs the following morning (number eaten = number placed in pen – number of whole eggs remaining). Three slimy sculpins (each >97 mm) died during the experiment (two in 1993 and one in 1994) and were replaced.

Head morphology of slimy and coastrange sculpins

We compared head morphology of the two sculpin species in an attempt to account for variation in feeding rates on eggs. The following measurements were made with electronic callipers (± 0.01 mm) from a broad size range of sculpins: (*i*) jaw protrusion (JPRO, distance from the middle of the jaw to the perpendicular intersection of a line joining the posterior extent of the jaw), (*ii*) jaw width (JW, greatest distance between the margins of the jaw), (*iii*) head length, (*iv*) head depth, (*v*) maximum head width, and (*vi*) head width at the eyes. We estimated mouth area (MA) by dividing the equation of the area of an ellipse by one half: $MA = \frac{1}{2}[\pi(JPRO \times \frac{1}{2}JW)]$ where JPRO and ½JW represent the two radii of the ellipse. We analyzed the morphological variation by ANCOVA of individual traits relative to body length.

Susceptibility of eggs to sculpin predation

We measured the susceptibility of salmon eggs to sculpin predation by a direct and indirect method. Indirectly, we monitored the "attractiveness" of fresh eggs contained in minnow traps to sculpins throughout the spawning period on three separate spawning beaches in 1993 (Woody Island, Fuel Dump Island, and Painted Rock on Porcupine Island).

Standard "Gee" minnow traps were baited with 40 g (± 1 g) of fresh eggs, which were encased in a Vibert incubation box (the eggs could be seen and smelled but not eaten). On each spawning beach, and within areas where sockeye were known to spawn, five stations were established 5 m apart along a 1.5-m depth transect marked with numbered white rocks. About every 2 days, at each station, a baited minnow trap was set 2–3 h before dusk and collected 14–18 h later. Each captured fish was identified to species, counted, a subsample measured (TL), and then all released back onto the spawning ground.

Direct estimates of sculpins in 112 sockeye female nests were made on Woody Island beach throughout the spawning period in both 1992 and 1993. Individual territorial sockeye females that had not yet completed spawning were first identified by snorkelers from a distance (i.e., nests were selected without knowledge of sculpin numbers). A 1-m^2 quadrat was placed around the centre of the nest and all sculpins within were counted. The presence or absence of eggs within the nest was also recorded.

Results

Temporal and spatial distribution of sculpins and sockeye salmon

Sockeye spawning activity occurred within a 21-day period. Females first began nest construction on 8 August (12 females within our twenty-four 5-m^2 sampling sites) and the last breeding female on the beach was noted on 29 August. After 8 August, the density of breeding females increased rapidly, with most females completing spawning between 9 and 17 August (Fig. 1B). Peak densities of breeding females of about 13 per 25 m^2 occurred on 11 and 13 August, just 3 and 5 days after the commencement of spawning. After these dates, the number of spawned-out females rose rapidly, with virtually no females remaining alive on the beach by the end of August (Fig. 1C).

Quantitative sampling of sculpins was started on 2 August, 6 days before the first sockeye females established territories. Even then, sculpins were more abundant on the portion of the beach where sockeye spawning activity would eventually occur compared with areas where spawning did not occur (Fig. 1A). Sculpin abundance increased in these areas in the days preceding 8 August, when sockeye females first established nest sites, and continued to increase until about 4 days after the density of breeding females peaked on 13 August. Sculpin abundance declined slightly in the sampling areas where little or no sockeye spawning activity was observed, although there were slight increases at the beginning and end of the sockeye spawning period. On the five sampling days from 13 to 23 August, sculpin abundance in the 10 sampling sites within the spawning area averaged 12.9/m^2 compared with 0.9/m^2 in the 14 sampling sites in the nonspawning areas, a 14.3-fold difference.

As the density of sockeye females began to decline after 23 August, so too did the density of sculpins (Fig. 1A). However, even after all sockeye were gone from the spawning beach, sculpin abundance remained higher in the area formerly used by the spawning sockeye (4.5/m^2 on 7 September) compared with those sites that were not used (1.0/m^2). At this time, no salmon eggs were visible and there were few salmon carcasses present, thus limiting sculpins' easy access to food.

All known sizes of both sculpin species were present in our study area, although the smallest observed (<50 mm TL) comprised less than 5% of the total. The three size-classes of sculpins we enumerated followed the same spatial and

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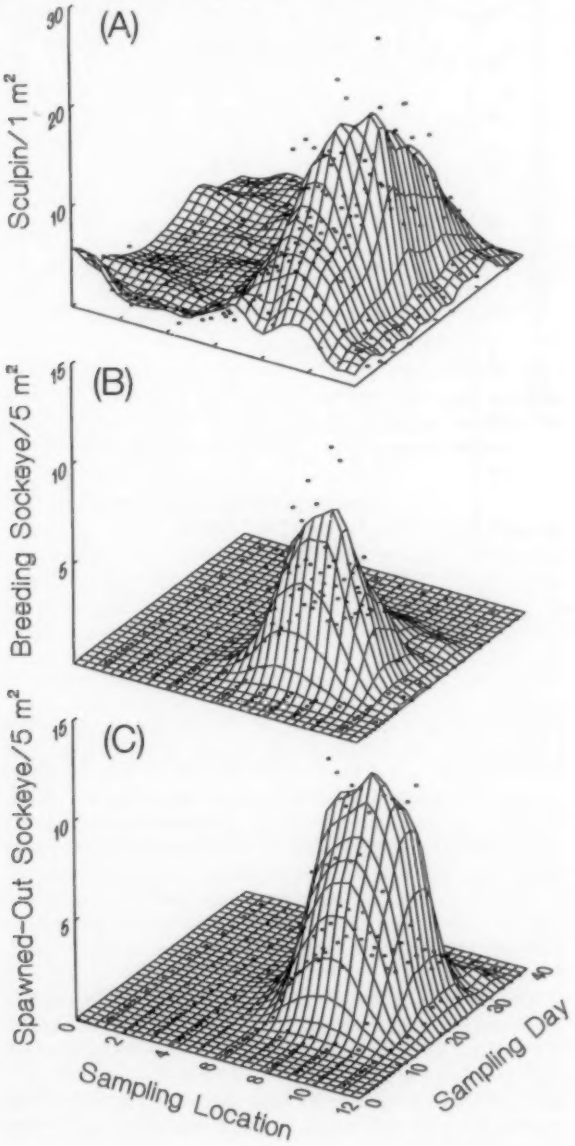
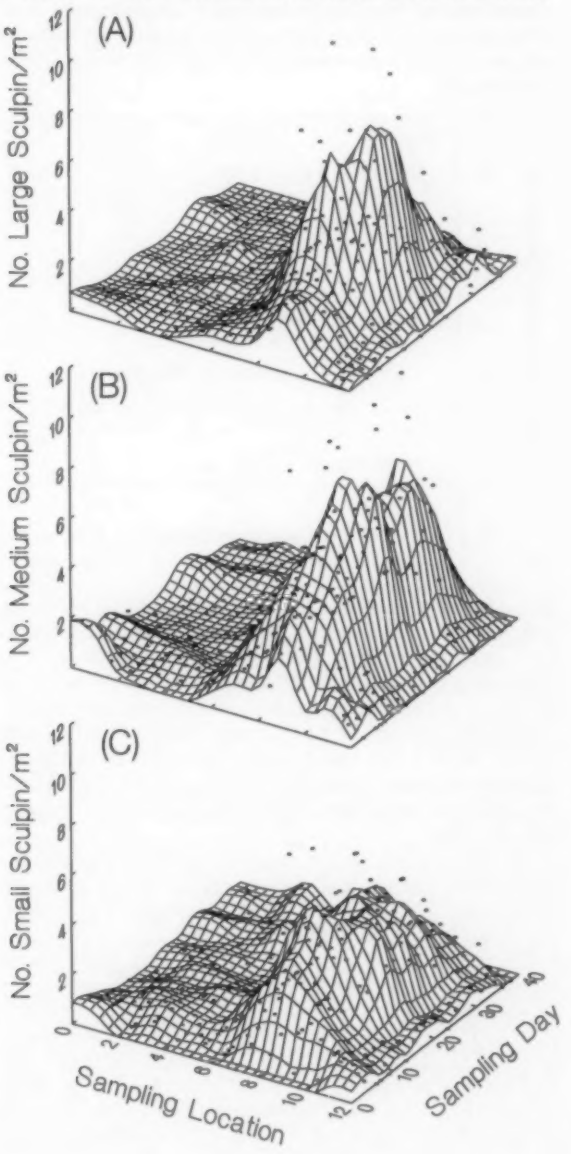
Fig. 1. Spatial and temporal distribution of sculpins and sockeye salmon females at Woody Island beach. Each point is the mean number of fish at the two sites (0.75 and 1.5 m depths) sampled at each of the 12 locations evenly spaced along 180 m of beach. Distance-weighted least squares analysis (SYSTAT, Inc.) was used for smoothing. (A) Sculpin density; (B) spawning sockeye female density; (C) density of sockeye females that have completed spawning. Sampling days start on 1 August.



temporal pattern in abundance as described above, although the medium (75–100 mm) and large (>100 mm) sculpins were more numerous on the spawning grounds, showed greater increases and decreases in numbers, and were found relatively less often outside the spawning area than small sculpins (50–75 mm) (Fig. 2).

Fig. 2. Spatial and temporal distribution of three size-classes of sculpins on Woody Island spawning beach: (A) large (>100 mm TL), (B) medium (76–100 mm TL), and (C) small (50–75 mm TL).



When the spatial and temporal distributions of sculpins and sockeye are viewed together, the near-perfect match in their distributions is clear (Figs. 1 and 2). The highest densities of sculpins occurred with the highest densities of breeding sockeye salmon. Sculpin density declined dramatically at the boundaries of the spawning area and was uniformly low outside it.

Length and condition of sculpins

The mean total length of both slimy and coastrange sculpins captured by dipnet in 1993 varied significantly over time

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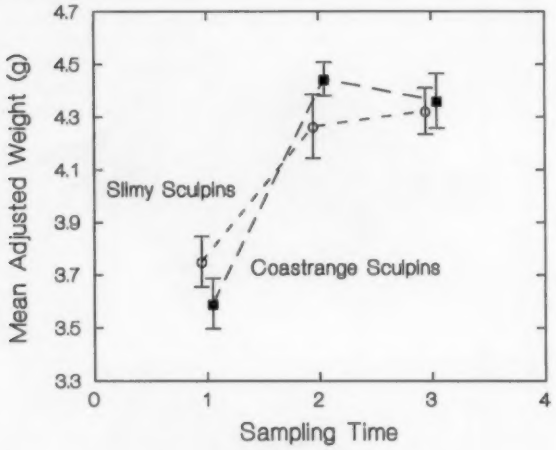
Fig. 3. Adjusted weight (± SE) of slimy sculpins (open circles) and coastrange sculpins (solid squares) captured on Woody Island beach before (1: 4–6 August), during (2: 14 August), and after (3: 1 September) the completion of spawning by sockeye salmon in 1993. Stomach contents are included in fish weights. Adjustments and analyses were done on natural logarithms of all measurements (see Methods).



($F_{2,284} = 7.96$, $P < 0.001$). Mean size was smallest before the arrival of the sockeye, largest during the presence of the sockeye, and intermediate afterwards (slimy: 64.38 ± 1.97 (SE) mm, $n = 40$, 75.77 ± 1.89 mm, $n = 51$, and 69.36 ± 1.50 SE mm, $n = 58$ for early, middle, and late samples, respectively; coastrange: 68.88 ± 1.69 mm, $n = 68$; 73.31 ± 2.42 mm, $n = 49$; 71.67 ± 2.42 mm, $n = 46$). There was no significant difference between species in size ($F_{1,284} = 0.64$, $P > 0.4$), nor was there any interaction between time and species ($F_{2,284} = 1.41$, $P > 0.2$).

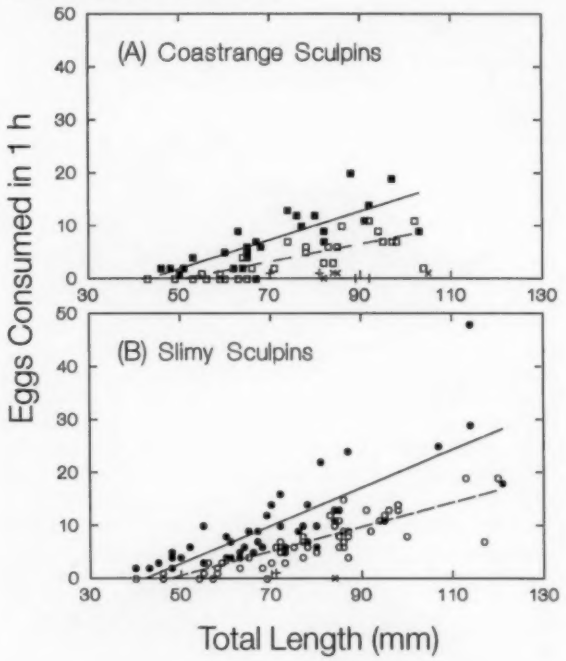
For both sculpin species, the slope of the relationship between lnWT and the lnTL did not differ over the collection times (slimy: $F_{2,172} = 1.72$, $P > 0.15$; coastrange: $F_{2,183} = 2.88$, $P = 0.06$), but line elevations did (slimy: $F_{2,174} = 5.72$, $P < 0.005$; coastrange: $F_{2,185} = 27.48$, $P < 0.001$). Both species showed a similar ($F_{1,284} = 0.09$, $P > 0.7$) and significant change in adjusted weight over time ($F_{2,284} = 30.89$, $P < 0.001$) (Fig. 3). There was no interaction between species and time of sampling ($F_{2,284} = 2.23$, $P > 0.1$). Fish collected during and after the spawning period were significantly heavier than those collected before spawning commenced (Tukey's test: $P < 0.01$ between sample 1 and each of 2 and 3; $P > 0.6$ between 2 and 3).

Egg consumption over a 1-h period

Both sculpin species readily ate water-hardened and fresh salmon eggs placed in front of them. The water-hardened eggs were heavier (0.124 ± 0.001 (SE) g, $n = 91$ versus 0.100 ± 0.001 g, $n = 69$) and had a greater diameter (6.17 ± 0.03 (SE) mm, $n = 92$ versus 5.73 ± 0.04 mm, $n = 71$) than fresh eggs. The average percent increase in egg weight and diameter for eggs of the same female was 9.5 and 3.2%, respectively ($n = 5$ females).

For slimy sculpins, there was a significant difference in the

Fig. 4. Regressions of the number of fresh (solid symbols) and water-hardened (open symbols) salmon eggs eaten by (A) coastrange sculpins and (B) slimy sculpins of different lengths in a 1-h period under controlled conditions. Outliers, those fish marked by ×'s and +'s for sculpins in the fresh and water-hardened egg treatments, respectively, were not included in regression calculations (see Methods). Analyses were done on the natural logarithms of both measurements.



slope of the regression of $\log_e$ of the number of eggs eaten versus $\log_e$ of fish length for fresh and water-hardened eggs (ANCOVA: $F_{1,97} = 4.24$, $P < 0.05$, $R^2 = 0.70$) (Fig. 4). Slimy sculpins ate nearly 1.5 times as many fresh eggs as water-hardened eggs on average, with the difference increasing with sculpin size. One of the largest slimy sculpins tested (114 mm) ate 48 fresh eggs within a 15-min period. Similarly, coastrange sculpins also consumed more fresh eggs than water-hardened eggs per fish size ($F_{1,43} = 24.06$, $P < 0.001$), but in this case, there was no significant difference in the slopes ($F_{1,42} = 0.054$, $P > 0.80$).

There were significant differences between the species in the number of both fresh and water-hardened eggs consumed in 1 h. Slimy sculpins ate more fresh and water-hardened eggs than coastrange sculpins ($F_{1,67} = 9.20$ and $F_{1,73} = 13.51$, $P < 0.005$), with no difference between species in the slope of the relationship with fish length in either case ($F_{1,66} = 2.63$ and $F_{1,72} = 0.80$, $P > 0.10$).

In both species, there was a lower limit in the size of fish that could consume water-hardened eggs (Fig. 4). These small fish repeatedly attempted to eat eggs, but were unable to get them into their mouths. In slimy sculpins, this lower size limit was about 50 mm TL whereas for coastrange sculpins the lower limit was about 55 mm. In contrast, all five coastrange sculpins tested that were <55 mm (46–53 mm) and all seven

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Fig. 5. Regression of the number of fresh salmon eggs eaten over a 7-day period versus fish length for slimy sculpins (open circles) and coastrange sculpins (solid squares).

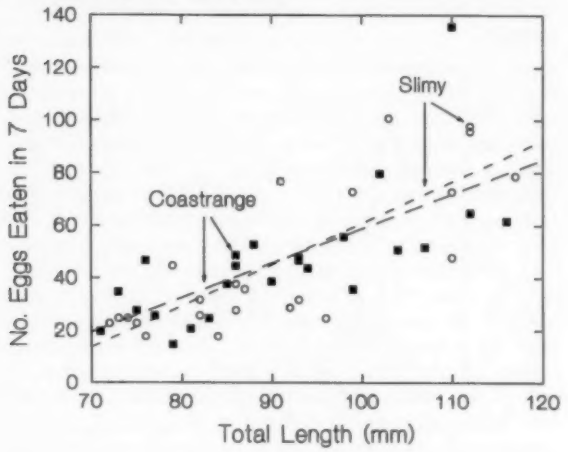
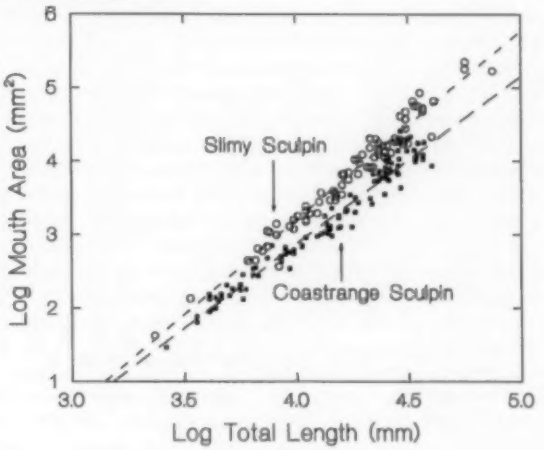


Fig. 6. Plot of mouth area versus total length of slimy sculpins (open circles) and coastrange sculpins (solid squares) captured on the island spawning beaches. See Methods for formula for calculating mouth area.



slimy sculpins tested that were <50 mm (40–48 mm) ate at least one fresh egg. Virtually all of the fresh eggs eaten by small sculpins were broken during ingestion whereas the water-hardened eggs rarely were, even by large sculpins.

Egg consumption over a 7-day period

The number of fresh eggs consumed by both sculpin species over 7 days was similar and positively dependent on body size (slimy sculpin: $y = 1.58TL - 96.79$, $R^2 = 0.63$, $n = 23$; coastrange sculpin: $y = 1.31TL - 72.42$, $R^2 = 0.49$, $n = 24$) (Fig. 5). There were no significant differences in slope (ANCOVA: $F_{1,43} = 0.460$, $P > 0.5$) or line elevation ($F_{1,44} = 0.006$, $P > 0.9$). For each species, independent of body size ($P > 0.1$, $R^2 < 0.15$), nearly half of all eggs consumed were eaten during the first feeding opportunity (slimy sculpin: 49.8 ± 2.5% (SE), $n = 23$; coastrange sculpin: 43.0 ± 2.7%, $n = 24$; $t = 1.85$, df = 45, $P = 0.072$).

Head morphology of slimy and coastrange sculpins

Slimy sculpins have wider jaws (and heads) than do coastrange sculpins at all sizes ($F_{1,180} = 42.8$, $P < 0.001$). Similarly, the jaws of slimy sculpins protrude further than those of coastrange sculpins over all sizes measured, with the difference increasing with increasing fish length ($F_{1,179} = 48.4$, $P < 0.001$). Taken together, slimy sculpins have greater jaw area than coastrange sculpins over all sizes, with the difference increasing with increasing size ($F_{1,179} = 19.9$, $P < 0.001$) (Fig. 6). This difference is consistent with the ability of slimy sculpins to consume water-hardened eggs at a smaller size than coastrange sculpins (Fig. 4).

Susceptibility of eggs to sculpin predation

In the days preceding the commencement of sockeye spawning on three separate island spawning beaches in 1993, we caught an average of 146.4 ± 27.6 (SE) ($n = 10$), 44.1 ± 8.9 ($n = 15$), and 142.6 ± 35.1 ($n = 5$) sculpins per egg-baited trap (Fig. 7). After sockeye spawning started on 8 August, the number of sculpins caught in traps dropped abruptly, reaching zero for consecutive sampling periods during peak sockeye spawning on two beaches. On all but Fuel Dump Island beach, the numbers of sculpins captured with egg-baited traps increased at the end of the sockeye spawning period. The pattern of capture in baited traps was similar and significant for both species of sculpin (Kruskal–Wallis test: $P < 0.001$). Coastrange comprised 61.5% of the sculpins captured. The average length of captured fish was 84.0 ± 0.4 (SE) mm ($n = 1133$) and 85.5 ± 0.3 mm ($n = 1518$) for slimy and coastrange sculpins, respectively.

The pattern in the number of sculpins found in individual sockeye female nests over the spawning season was similar to that observed in the minnow traps. There were distinctly more sculpins in the nests of the earliest and latest females to spawn than there were in the nests of those spawning during the main part of the spawning period (Fig. 8). In 1992, rough weather prevented quantification of the sculpins per nest of the earliest breeding females. However, we observed one of the first females to spawn on 9 August and noted that her nest contained more than 100 sculpins. After this date, the number of sculpins per nest dropped, but at the end of the run, we quantified a large number (71.3 ± 16.1 (SE), $n = 4$) of sculpins per nest. In 1993, we purposely concentrated our sampling on the early part of the spawning run to quantify what we had missed in 1992. The number of sculpins per nest with eggs was 66.1 ± 7.0 ($n = 6$) over the first 3 days of spawning and then dropped significantly.

In both 1992 and 1993, there was a significant effect of sampling date and whether or not eggs were present in the nest on the number of sculpins present, with no interaction between the two factors (1992: egg, $F_{1,75} = 5.37$, $P < 0.05$; day, $F_{1,75} = 17.44$; $R^2 = 0.31$; 1993: egg, $F_{1,31} = 16.66$, $P < 0.001$; day, $F_{1,31} = 12.30$; $R^2 = 0.46$, $P = 0.001$). In both years, there were over twice as many sculpins in the nests containing eggs (nests without eggs: 8.93 ± 1.26 (SE), $n = 29$ and 17.67 ± 2.51, $n = 12$ for 1992 and 1993, respectively; nests with eggs: 23.00 ± 2.92, $n = 49$ and 38.82 ± 4.54, $n = 22$).

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Fig. 7. Mean number (± SE) of sculpins captured in sets of five minnow traps baited with 40 g of fresh salmon eggs set on three separate sockeye salmon island beach spawning locations in Iliamna Lake, Alaska, over the month of August 1993.

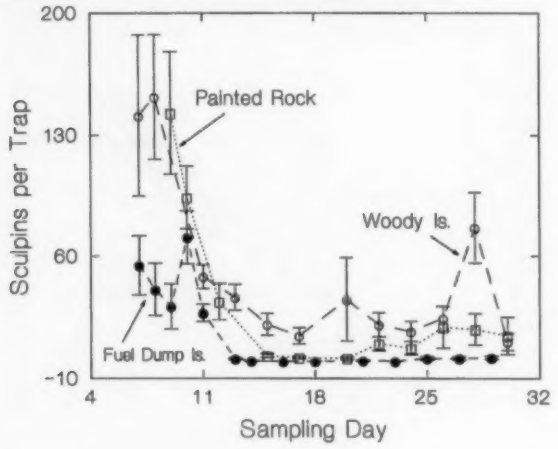
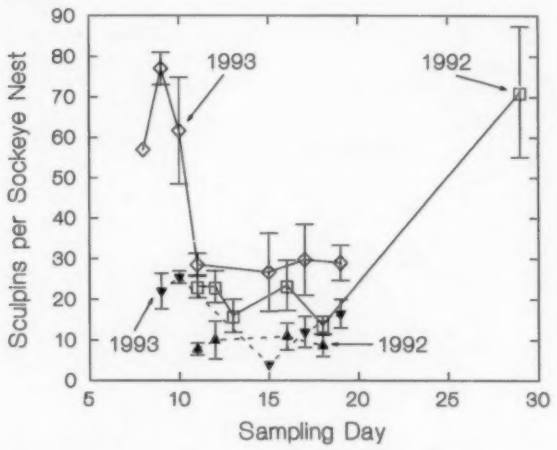


Fig. 8. Mean number of sculpins (± SE) observed in the nests of breeding sockeye females (1 m^2) over the course of the spawning season in 1992 and 1993. Nests in which eggs were found are shown by open symbols; nests without eggs are shown by solid symbols.



Discussion

Relationship between sockeye spawning and sculpin density

The spawning of sockeye salmon on island beaches in Iliamna Lake is predictable in space and time. Commencement date of spawning usually varies by only a few days over years (e.g., Quinn and Foote 1994; this study). Spawning site locations are also highly predictable over a broad scale (kilometres, Blair et al. 1993) and a very fine scale (metres, Hendry et al. 1995). Our results indicate that slimy and coastrange sculpins make significant use of this highly predictable resource by feeding extensively on salmon eggs.

Salmonid eggs are likely a valuable resource for sculpins. They are abundant, easy to catch, and require little handling (see Biga 1996) and are energy rich (about 6200 cal/g dry egg (1 cal = 4.1868 J), Wetzel 1993). Further, their availability in late summer before the long Alaskan winter probably increases their importance in the ecology of the sculpins. The amount of fall energy stores in freshwater fishes can have a direct effect on overwinter survival (Gardiner and Geddes 1980; Smith and Griffith 1994) and on reproduction the following year (Meffe and Snelson 1993). When sculpins arrived on the beach in early August, their condition appeared low, even though the majority of the summer and the associated feeding opportunities were past, and then increased substantially with the spawning of the salmon (Fig. 3). Hershey and McDonald (1985) noted that larger slimy sculpins appeared to be food limited in Toolik Lake, Alaska, and linked this to the exponential increase in rate of mortality of larger sculpins once they reached maturity. If older Iliamna Lake sculpins are also food limited, and unable to recoup the energy losses associated with their late spring and early summer spawning period (Craig and Wells 1976), then an abundant egg resource will likely have significant effects on overwinter survival and future reproduction.

Sculpin numbers increased dramatically over the course of the salmon spawning run on Woody Island and decreased in a less dramatic fashion after spawning completion (Fig. 1A). The increase was noted days before the commencement of sockeye spawning and was apparent only on the spawning beach itself and not on directly adjacent habitats. This spawning site specific increase suggests that sculpins may predict the arrival of the egg resource, and do not simply react to its presence. We know from in situ experiments on Woody Island that sculpins are highly attracted to the odor of fresh sockeye eggs (Dittman et al. 1998) and to the digging actions of females during nest construction (C.J. Foote and G.S. Brown, personal observation; see also Janssen 1990). However, neither event occurred during the first 6 days of our observations, yet sculpin numbers still increased. Salmon increasingly gathered and schooled around the spawning area before settling, but their movements were broad and carried them all around the inner bay, including nonspawning areas. The fact that sculpin numbers increased only in the eventual sockeye spawning area suggests that visual cues of the positions of the schooling sockeye were also not the cues for directed movement by the sculpins. However, it is possible that sculpins were detecting residual cues of previous spawning in the area, as has been shown in lake trout (*Salvelinus namaycush*) (Foster 1985), or had simply learned where the spawning area was from previous experience. Sculpins live up to 8 years in Iliamna Lake (Roger 1971), and hence have repeated opportunities to learn the temporal and spatial distribution of egg resources.

McDonald et al. (1982) reported densities of slimy sculpins in the range of 0.44–2.58/m^2 in rocky littoral areas in Toolik Lake, Alaska. These densities are similar to those that we found in the rocky littoral areas not occupied by salmon, but far below those on the adjacent spawning grounds during peak spawning (Fig. 1A). Given the high peak sculpin densities observed on the spawning beach, it seems likely that sculpins must be arriving from relatively large distances. Significant sculpin migrations (kilometres) have been noted previously in relation to the activities of salmon (Reed 1967; McLarney 1967). However, such movements likely increase their risk of

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predation (Brown 1991). In Iliamna Lake, four major sculpin predators, lake trout, Arctic char (*Salvelinus alpinus*), burbot (*Lota lota*), and rainbow trout (*Oncorhynchus mykiss*), are present. On the beaches, sculpins are also accessible to the common merganser (*Mergus merganser*) (Sjöberg 1988).

Sculpins may start their movement to sockeye spawning beaches before the commencement of spawning to maximize their access to the egg resource. The spawning period of island beach spawning sockeye is short (Fig. 1B), with individual females completing spawning in 1–2 days (Quinn and Foote 1994) and most females having completed spawning within a week. If sculpins relied solely on cues of actual spawnings to move to the spawning sites, they could miss feeding opportunities during the time it takes to move to that location.

Sculpins can also increase their access to sockeye eggs by being in nests during spawning events, as this is when the eggs are most available. At spawning, the eggs (about 500–1000 per spawning) are exposed and the easiest to capture. We have shown that sculpins can eat a large number of eggs within minutes of their discovery, particularly if they are freshly spawned (Fig. 4). However, shortly after spawning, the number of eggs that can be consumed drops for two reasons. First, a spawning act lasts only seconds, and over about the next 10 min the female covers the eggs with gravel. Although the eggs within the nest may remain accessible to the sculpins buried with them, they may not be easily localized or accessible to other sculpins. Second, the eggs immediately start to swell and harden, with the process largely complete within an hour of spawning. Consequently, the size range of sculpins that can consume these eggs decreases due to gape limitations (Fig. 6), and those still able can consume fewer of them (Fig. 4). The digestion rate of these water-hardened eggs is also slower than that of freshly spawned eggs (McLarney 1967), further limiting the number of eggs that can be consumed. Gape limitation may account for the relatively low proportion of small sculpins on the spawning grounds (Fig. 2) and act to select for the large egg size of beach spawning sockeye.

Potential effects of egg predation on sockeye salmon

The potential impact of sculpin predation on sockeye production was shown clearly in the feeding experiments. Both species of sculpin readily consumed eggs, with the number consumed being directly related to fish size and the state (fresh versus water hardened) of the eggs. Indeed, they appeared to gorge on eggs at the first opportunity. For example, large sculpins could easily consume over 20 fresh eggs, and up to 48, within minutes of their discovery.

The potential number of eggs consumed over the spawning season was also directly related to sculpin size. The largest sculpins of both species could consume over 80 fresh eggs, and up to 135, over a 7-day period. While we do not know how many eggs individual sculpins are consuming over the course of the spawning run, we suspect for a number of reasons that they are feeding to near satiation. First, we often noted that sculpins were bloated with eggs during our surveys. Second, their high motivation to feed on eggs was apparent in our feeding studies, where they readily fed on eggs in unnatural conditions and in broad daylight. Sculpins are typically thought to be nocturnal (e.g., Selgeby 1988), but we observed that they were active on the beaches throughout the day. Third, the marked decline in the number of sculpins captured in egg-baited traps coincident with the marked increase in the condition of sculpins after spawning commenced (Figs. 3 and 7) suggests that sculpins are finding plenty of eggs to consume outside the traps.

With the data from the beach surveys, our feeding experiments, and from our size estimates of the sculpins on Woody Island beach, we can derive an estimate of the number of sockeye eggs consumed by sculpins. There were about 1000 females on the beach in 1992. We estimated the presence of 844 females in 1990 (Quinn and Foote 1994), and the overall density and numbers appeared similar. Woody Island sockeye females have an average of about 3800 eggs (Blair et al. 1993), indicating that the total number of eggs deposited would be about 3 800 000. Using the average density of sculpins observed on the spawning grounds during their peak abundance (13.5/m^2; data from August 13, 15, and 17) and an estimate of overall spawning area of about 1200 m^2 (80 m along the shoreline by 15 m out), we estimate that there were about 16 200 sculpins on the beach. To estimate fresh egg consumption, we use an average sculpin size of 85 mm derived from our trap data in 1993, which is consistent with survey data of 1992 (Fig. 2), although larger than those captured by dip net in 1993. Sculpins of this size can consume about 38 fresh eggs over 1 week (Fig. 5), a period that encompasses the majority of sockeye spawning. Taken together, we estimate that about 617 220 or about 16% of the eggs laid may have been consumed by sculpins. The estimate would be higher if total consumption by sculpins were extrapolated over 14 days (25%, based on a consumption of 58.3 eggs per sculpin, C.J. Foote and G.S. Brown, unpublished data), but it would be lower if sculpin predation were not assumed to be on fresh eggs. However, the presence of significant numbers of sculpins in the nests at the time of spawning indicates that the majority of the predation probably occurs within minutes of spawning.

McLarney (1967) estimated that sculpins could take 7% of the eggs available in pink salmon (*Oncorhynchus gorbuscha*) spawning runs, even when the density of sculpins was much lower than we noted and the gravel much less penetrable. The majority of eggs were taken in the stream drift, dislodged during nest superimposition by females, and unlikely to have survived in any case. In contrast, on the island beaches, egg predation by sculpins seems to be principally on viable salmon eggs. Nest superimposition appears uncommon given the brief spawning period, the relatively long mean life span of breeding females (7.4 days), and the rarity of female displacement (Quinn and Foote 1994).

Selective nature of sculpin predation on sockeye eggs

The intensity of sculpin predation on sockeye eggs varied substantially over the course of the spawning run. Females that spawned early and, to a lesser degree, late in the run were subject to far greater numbers of sculpins in their nests than those in the middle of the run (Fig. 8), and hence undoubtedly suffered the greatest egg predation. This conclusion is supported by the similar temporal pattern of capture of sculpins in egg-baited minnow traps (Fig. 7). A set number of eggs early and late in the spawning run attracted more sculpins, and hence seemed more vulnerable to predation, than those in the middle of the spawning period. Further, the difference in the intensity of predation is probably greater than that indicated by

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differences in the number of sculpins per nest alone. Sculpins captured before spawning started had a significantly lower condition factor than those collected during the run. Given that egg digestion takes many days (McLarney 1967) and that sculpins readily gorge on a large portion (>40%) of the eggs that they will consume at their first opportunity, then individual sculpins that are in sockeye nests early in the spawning run are likely to be hungrier and to eat more eggs than those observed in the nests later on.

The temporal nature of sculpin predation on eggs in the nests of individual females may account for the relatively short spawning season of sockeye salmon on island beach spawning locations in Iliamna Lake (Hendry et al. 1995; Fig. 1B). In 1992, peak spawning was observed within 6 days of the first female spawning, and the majority of females appeared to spawn over a 6- to 10-day period. This is in contrast with stream spawners in sockeye salmon where runs are typically much more extended, including those in Alaska and other parts of Iliamna Lake, lasting 3–6 weeks and sometimes longer (e.g., Demory et al. 1964; Wood and Foote 1996). Sweeney and Vannote (1982) argued that the "predator satiation" hypothesis accounted for the marked synchrony in adult emergence patterns in mayflies, and the same argument appears to apply here. They showed that the percentage of adults succumbing to predators on a given day was inversely related to the total number of adults available as prey each day, which agrees with what we found relative to sculpin predation in sockeye nests. The interesting conclusion from our study is that the abundance of predators over time alone does not reveal the temporal nature of egg predation. In that case, peak sculpin and sockeye numbers coincide. Rather, it is the independent temporal measures of the sculpins per nest and the attraction of sculpins to egg-baited traps that indicate this pattern of selective predation.

The question remains as to how sculpins could potentially have such significant predatory and demographic effects on sockeye salmon spawning on the island beaches when their effects are usually not considered significant in stream habitats (e.g., Moyle 1977). We believe the answer lies in the large substrate on the island beaches. Leonetti (1997) reported geometric mean particle sizes between 35 and 79 mm on Woody Island and Fuel Dump Island spawning beaches, with particles of <13 mm virtually absent (0.6%). Given that sculpins can penetrate cobble and gravel with significant interstices (Phillips and Claire 1966; McLarney 1967; Biga 1996), this porous substrate makes the developing eggs susceptible to sculpin predation while at the same time providing refuge for sculpins from their own predators.

The predictable, temporally and spatially clumped resource of salmon eggs available on the spawning beaches of Iliamna Lake is an important factor shaping the ecology of the two resident sculpin species. They, in turn, appear to have shaped the spawning behavior of the sockeye salmon, specifically their compressed spawning season. Through sculpins, an important exogenous energy source in the form of sockeye eggs is incorporated into the piscivore populations.

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References

Biga, H.C. 1996. Sculpins as predators of lake trout eggs and larvae; an assessment of their predatory capabilities and constraints. M.S. thesis, Loyola University, Chicago, Ill.

Bilby, R.E., Fransen, B.R., and Bisson, P.A. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. Can. J. Fish. Aquat. Sci. **53**: 164–173.

Blair, G.R., Rogers, D.E., and Quinn, T.P. 1993. Variation in life history characteristics and morphology of sockeye salmon in the Kvichak River system, Bristol Bay, Alaska. Trans. Am. Fish. Soc. **122**: 550–559.

Brown, L.R. 1991. Differences in habitat choice and behavior among three species of sculpin (*Cottus*) in artificial stream channels. Copeia, 1991: 810–819.

Cone, R.S. 1986. The need to reconsider the use of condition indices in fishery science. Trans. Am. Fish. Soc. **118**: 510–514.

Craig, P.C., and Wells, J. 1976. Life history notes for a population of slimy sculpin (*Cottus cognatus*) in an Alaskan arctic stream. J. Fish. Res. Board Can. **33**: 1639–1642.

Demory, R.L., Orrel, R.F., and Heinle, D.F. 1964. Spawning ground catalog of the Kvichak River system, Bristol Bay, Alaska. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. No. 488.

Dittman, A., Brown, G.S., and Foote, C.J. 1998. The role of chemoreception in salmon egg predation by coastrange (*Cottus aleuticus*) and slimy sculpins (*C. cognatus*) in Iliamna Lake, Alaska. Can. J. Zool. **76**. In press.

Eggers, D.M., and Rogers, D.E. 1987. The cycle of runs of sockeye salmon (*Oncorhynchus nerka* Walbaum) to the Kvichak River, Bristol Bay, Alaska: cyclic dominance or depensatory fishing? *In* Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. *Edited by* H.D. Smith, L. Margolis, and C.C. Wood. Can. Spec. Pub. Fish. Aquat. Sci. No. 96. pp. 343–366.

Foster, N.R. 1985. Lake trout reproductive behavior: the influence of chemosensory cues from young-of-the-year by-products. Trans. Am. Fish. Soc. **114**: 794–803.

Furness, R.W., and Monaghan, P. 1987. Seabird ecology. Chapman and Hall, New York.

Gardiner, W.R., and Geddes, P. 1980. The influence of body composition on the survival of juvenile salmon. Hydrobiologia, **154**: 3–11.

Hendry, A.P., Leonetti, F.E., and Quinn, T.P. 1995. Spatial and temporal isolating mechanisms: the formation of discrete breeding aggregations of sockeye salmon (*Oncorhynchus nerka*). Can. J. Zool. **73**: 339–352.

Hershey, A.E., and McDonald, M.E. 1985. Diet and digestion rates of slimy sculpins, *Cottus cognatus*, in an Alaskan arctic lake. Can. J. Fish. Aquat. Sci. **42**: 483–487.

Janssen, J. 1990. Localization of substrate vibrations by the mottled sculpin (*Cottus bairdi*). Copeia, 1990: 349–355.

Kerns, O.R., and Donaldson, J.R. 1968. Behavior and distribution of spawning sockeye salmon on island beaches in Iliamna Lake, Alaska, 1965. J. Fish. Res. Board Can. **25**: 485–494.

Kline, T.C., Jr., Goering, J.J., Mathisen, O.A., Poe, P.H., Parker, P.L., and Scalan, R.S. 1993. Recycling of elements transported upstream by runs of Pacific salmon: II. $\delta^{15}N$ and $\delta^{13}C$ evidence in the Kvichak River watershed, Bristol Bay, Southwestern Alaska. Can. J. Fish. Aquat. Sci. **50**: 2350–2365.

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Leonetti, F.E. 1997. Estimation of surface and intergravel water flow at sockeye salmon spawning beaches in Iliamna Lake, Alaska. N. Am. J. Fish. Manage. **17**: 194–201.

McDonald, M.E., Cuker, B.E., and Mozley, S.C. 1982. Distribution, production, and age structure of slimy sculpin in an arctic lake. Environ. Biol. Fishes, **7**: 171–176.

McLarney, W.O. 1967. Intra-stream movement, feeding habits, and population of the coastrange sculpin, *Cottus aleuticus*, in relation to eggs of the pink salmon, *Oncorhynchus gorbuscha*, in Alaska. Ph.D. thesis, University of Michigan, Ann Arbor, Mich.

Meffe, G.K., and Snelson, F.F., Jr. 1993. Lipid dynamics during reproduction in two livebearing fishes, *Gambusia holbrooki* and *Poecilia latipinna*. Can. J. Fish. Aquat. Sci. **50**: 2185–2191.

Moyle, P.B. 1977. In defense of sculpins. Fisheries (Bethesda), **2**: 20–23.

Northcote, T.G. 1954. Observations on the comparative ecology of two species of fish, *Cottus asper* and *Cottus rhototheus*, in British Columbia. Copeia, **1**: 25–28.

Phillips, R.W., and Claire, E.W. 1966. Intragravel movements of the reticulate sculpin, *Cottus perplexus*, and its potential as a predator on salmonid embryos. Trans. Am. Fish. Soc. **95**: 210–212.

Quinn, T.P., and Foote, C.J. 1994. The effects of body size and sexual dimorphism on the reproductive behavior of sockeye salmon, *Oncorhynchus nerka*. Anim. Behav. **48**: 751–761.

Quinn, T.P., Hendry, A.P., and Wetzel, L.A. 1995. The influence of life history trade-offs and the size of incubation gravels on egg size variation in sockeye salmon (*Oncorhynchus nerka*). Oikos, **74**: 425–438.

Reed, R.J. 1967. Observations of fishes associated with spawning salmon. Trans. Am. Fish. Soc. **96**: 62–67.

Roger, P.B. 1971. The ecology of two species of cottids in Iliamna Lake, Alaska, and their relation to sockeye salmon. Master's thesis, University of Washington, Seattle, Wash.

Savino, J.F., and Henry, M.G. 1991. Feeding rate of slimy sculpin and burbot on young lake charr in laboratory reefs. Environ. Biol. Fishes, **31**: 275–282.

Selgeby, J.H. 1988. Comparative biology of the sculpins of Lake Superior. J. Great Lakes Res. **14**: 44–51.

Sjöberg, K. 1988. Food selection, food seeking patterns and hunting success of captive goosanders *Mergus merganser* and red-breasted mergansers *M. serrator* in relation to the behavior of their prey. Ibis, **130**: 79–93.

Smith, R.W., and Griffith, J.S. 1994. Survival of rainbow trout during first winter in Henry's Fork of the Snake River, Idaho. Trans. Am. Fish. Soc. **123**: 747–756.

Sweeney, B.W., and Vannote, R.L. 1982. Population synchrony in mayflies: a predator satiation hypothesis. Evolution, **36**: 810–821.

Wetzel, L.A. 1993. Genetic, morphometric, and life history characteristics of sockeye salmon (*Oncorhynchus nerka*) in the Wood River Lake system, Alaska. Master's thesis, University of Washington, Seattle, Wash.

Willson, M.F., and Halupka, K.C. 1995. Anadromous fish as keystone species in vertebrate communities. Conserv. Biol. **9**: 489–497.

Wood, C.C., and Foote, C.J. 1996. Evidence for sympatric genetic divergence of anadromous and nonanadromous morphs of sockeye salmon (*Oncorhynchus nerka*). Evolution, **50**: 1265–1279.

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Effects of chronic sublethal ammonia and a simulated summer global warming scenario: protein synthesis in juvenile rainbow trout (*Oncorhynchus mykiss*)

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Abstract: Protein synthesis, net accretion, and degradation in liver, gill, and white muscle and ribosomal translational efficiency and protein synthesis capacity in liver and gill were measured using a flooding dose of [^{3}H]phenylalanine in juvenile rainbow trout (*Oncorhynchus mykiss*). The fish were chronically exposed (90 days) in hardwater to the presence or absence of sublethal ammonia (70 μmol total ammonia·L^{-1}) alone or in combination with a 2°C elevation in the normal temperature profile over the months of June–September 1993 (ambient temperature range 13–22°C). Chronic sublethal exposure to ammonia had little impact on gill protein synthesis and degradation (protein turnover) and even less in muscle. However, in the liver, both protein synthesis and degradation were stimulated following 60 days of the sublethal ammonia exposure. The 2°C elevation in temperature resulted in a slight increase in protein turnover in both gills and liver. However, during the period of peak water temperature, the 2°C elevation in temperature inhibited protein dynamics in these tissues. Overall, elevated environmental ammonia in combination with a summer global warming scenario would challenge the ability of fish to adapt to alterations in the quality of their environment, most notably during periods of peak temperatures.

Résumé : La synthèse des protéines, leur augmentation et leur altération nettes, dans le foie, les branchies et les muscles blancs, l'efficacité de la traduction ribosomique, et la capacité de synthèse protéinique du foie et des branchies, ont été mesurés à l'aide d'une dose massive de phénylalanine[H^3] chez des truites arc-en-ciel juvéniles (*Oncorhynchus mykiss*). Les poissons ont été exposés de façon chronique (90 jours) en eau dure à la présence ou à l'absence d'une dose sublétale d'ammoniac (70 μmol d'ammoniac total·L^{-1}), seule ou combinée à une élévation de 2°C du profil normal de température entre juin et septembre 1993 (plage de température ambiante de 13 à 22°C). Une exposition sublétale chronique à l'ammoniac a eu peu d'effet sur la synthèse et la dégradation (renouvellement) des protéines dans les branchies et encore moins dans les muscles. Toutefois, dans le foie, la synthèse et la dégradation des protéines ont été stimulées après 60 jours d'exposition à une dose sublétale d'ammoniac. La hausse de 2°C de la température s'est traduite par une légère augmentation du renouvellement des protéines dans les branchies et dans le foie. Toutefois, pendant la période où la température de l'eau était maximale, l'élévation de 2°C de la température a inhibé la dynamique des protéines dans ces tissus. En général, une concentration élevée d'ammoniac dans l'environnement, associée à un scénario de réchauffement global en été, met à l'épreuve la capacité du poisson à s'adapter aux altérations de la qualité de son environnement, surtout pendant les périodes de températures extrêmes. [Traduit par la Rédaction]

Introduction

Freshwater fish are exclusively poikilothermic, and therefore, their body temperature is essentially identical to, and set by, the temperature of the water in which they live. Temperature is the single most important factor determining their metabolic rate (i.e., cost of living), which in turn influences a variety of physiological variables ranging from reproductive rate to growth rate to swimming performance (see Reid et al. 1995). The effects of climate change on fish and fisheries are therefore likely to be substantial, and yet, little attention has been drawn towards its impact on freshwater populations (Schindler et al. 1990). Furthermore, there are little or no hard experimental data on the chronic effects of relatively small temperature elevations on freshwater fish species over the annual cycle (see Reid et al. 1997*b*). Indeed, most of the biological data available to climate change modellers do not satisfactorily reflect real-world conditions (DeAngelis and Cushman 1990; Regier et al. 1990). Furthermore, perhaps the most important water quality issue in Canada today is contamination; most aquatic organisms no longer live in a pristine environment. There are virtually no data on how the effects of incremental temperature changes will interact with the effects of anthropogenic toxicants. This was the rationale behind a project that our laboratory initiated to examine the physiological impact on freshwater fish of exposure to a reasonable proximation of the global warming scenario (Mohnen and Wang 1992). Juvenile rainbow trout (*Oncorhynchus mykiss*) were chronically exposed to a small increase (+2°C) in water temperature superimposed upon the natural temperature profile representative of

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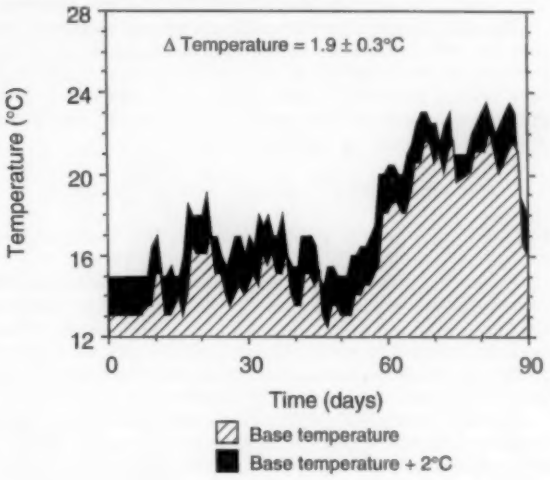
Fig. 1. Temperature profile for the hardwater exposure system during the 90-day experiment that ran over the summer of 1993 from June 18 (day 0) to September 15 (day 90). Juvenile rainbow trout were exposed to the natural daily and seasonal temperature variability representative of inshore Lake Ontario. Daily measurements were made on test tanks receiving base temperature water or the base temperature raised by 2°C.



inshore Lake Ontario. In addition, the effects of the elevation in the natural thermal regime were studied alone and in combination with sublethal, environmentally realistic concentrations of two common pollutants: low water pH (in softwater) and ammonia (in hardwater). Reid et al. (1995, 1997*a*) have provided an overview of the project as a whole, Dockray et al. (1996) have presented specific details on the physiological responses to the low pH–warming regime, and Linton et al. (1997) have presented parallel information on the physiological responses to the elevated ammonia–warming regime.

The objective of the present study was to determine the metabolic costs of a combination of increased temperature and elevated ammonia on fish as measured by tissue protein dynamics. The study parallels that of Reid et al. (1997*a*) on tissue protein dynamics of trout under the low pH–warming regime in softwater. It is generally believed that exposure to an environmental stressor and particularly adaptation to extreme environments are associated with increased metabolic costs (Calow 1991). Such shifts in the energy budget towards the defense of the internal environment suggest that less energy is available for other processes such as growth, activity, and reproduction. Protein dynamics were measured, as any change in the ability of the animal to grow, maintain electrolyte homeostasis, or increase fuel utilization might well be reflected in alterations in protein synthesis, accretion, or degradation in tissues directly or indirectly affected by the environmental stressor. In addition, it has been shown that a correlation exists between protein synthesis and metabolic rate in fish (Jobling 1985; Houlihan 1991) and that protein turnover rates are altered during and after exposure to toxicants (see Reid et al. 1997*b*).

The effects of chronic exposure to sublethal ammonia exposure are well documented and include alterations in gill morphology, reduced food uptake assimilation and growth, hypoglycaemia, increased liver glycogen and plasma Na^+ concentration, and reduced haemoglobin oxygen-carrying capacity (see Linton et al. 1997). These effects could result in or be the result of increased metabolic costs. The majority of these studies were conducted at total ammonia concentrations that were not environmentally realistic and were considerably higher than that used in the present and companion study (Linton et al. 1997). However, despite these differences, we predicted that the combination of elevated temperature and chronic sublethal ammonia would result in significant alterations in tissue protein dynamics, the cost of which could represent a serious challenge to the animals' ability to adapt to these and other changes in the quality of their environment.

Materials and methods

Experimental animals

Approximately 1600 rainbow trout of both sexes weighing initially 2–5 g were obtained April 19, 1993, from Rainbow Springs Hatchery (Thamesford, Ont.). Fish were held in two 600-L fiberglass tanks supplied at a rate of 2.5 $L \cdot min^{-1}$ with dechlorinated Hamilton tap water (moderately hard water: $[Ca^{2+}] = 1.95 \pm 0.22$ $mequiv. \cdot L^{-1}$, $[Na^+] = 0.56 \pm 0.03$ $mequiv. \cdot L^{-1}$, pH = 7.4–7.8) at the city supply temperature (inshore Lake Ontario; initially 11°C). During this initial holding period (6 weeks), fish were fed dry trout pellets (Zeigler, Salmon Starter) at a ration of 1% of body weight per day (wet weight basis). During the chronic exposures, fish were hand-fed to satiation twice daily as detailed in Dockray et al. (1996). Photoperiod was controlled and was adjusted weekly to mimic the natural photoperiod during the course of acclimation and chronic exposure.

Chronic exposure to elevated temperature and total ammonia

Fish were exposed for 90 days (starting on June 18, 1993, and ending on September 15, 1993) to one of four combinations of temperature and total ammonia in replicated tanks (eight 270-L tanks; 150 fish per tank) continuously supplied with aerated City of Hamilton dechlorinated tap water at 2.5 $L \cdot min^{-1}$. The four treatments were ambient water temperature (referred to as the "base" water temperature treatment) or base temperature raised by 2°C (base+2°C), each with or without an additional 70 μM total ammonia (base+Am and base+2°C+Am, respectively). Heat (+2°C) was added to the water using a countercurrent heat exchanger as detailed in Reid et al. (1995).

When exposures were started in mid-June, base and base+2°C water temperatures were 13 and 15°C, respectively (Fig. 1). During the initial 30 days, average water temperature rose only slightly. However, the day-to-day variability in temperature was as much as 4°C during this time, with peak temperatures reaching 17 and 19°C in the base and base+2°C treatment groups, respectively. The second 30-day period (days 30–60) was characterized by a gradual decline in water temperature in both treatment groups as the water temperature fell by approximately 2°C over the first 20 days of this period. However, the greatest increase in temperature was observed during the subsequent 10 days of this period as water temperatures rose rapidly by 5.5°C in both the base and base+2°C treatment groups. The highest water temperatures were reached during the final 30 days of this study (days 60–90), reaching peak temperatures of 22 and 23.5°C in the base and base+2°C exposure groups. Following 20–23 days of extreme temperature, water temperature fell dramatically over the final days of the experiment. During this period, fish experienced the single largest drop in water temperature as it fell by 5°C in both the base and base+2°C treatment groups.

Ammonia (total ammonia = $NH_4^+ + NH_3$) was added using mariotte bottles that were adjusted manually to deliver a 0.05 M $(NH_4)_2SO_4$ stock at an appropriate rate to achieve a nominal water

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total ammonia of 70 μmol·L^{-1}. Ammonia concentrations in water were monitored by the salicylate–hypochlorite method of Verdouw et al. (1978). Ambient water total ammonia was found to be 5.9 ± 0.63 (35) μmol·L^{-1}. The ammonia concentrations in the treatment groups exposed to elevated total ammonia were within approximately 20% of the nominal concentration (70 μmol·L^{-1}), with individual tank concentrations ranging from 58.2 ± 5.6 (10) to 78.6 ± 7.6 (10) μmol·L^{-1}. The elevation of water total ammonia had no influence on water pH, and water partial pressure of O_2 (P_{O_2}) was maintained well above 100 Torr (1 Torr = 133.322 Pa), with in-tank P_{O_2}s ranging from 121.3 ± 4.1 (15) to 134.6 ± 3.9 (15) Torr. In-tank water pH was monitored manually as described in Dockray et al. (1996) and ranged from 7.4 to 7.8 (mean = 7.6 ± 0.26). A detailed analysis of in-tank water quality for all eight tanks is presented in Linton et al. (1997).

Rates of protein synthesis, accretion, and degradation

Protein synthesis, accretion, and degradation rates in branchial baskets, liver, and white muscle were determined for temperature controls and their respective treatment groups before starting (day 0) and at 30, 60, and 90 days of exposure.

Tissue protein synthesis was determined from the incorporation of radioactive phenylalanine based on the method of Garlick et al. (1980), which was modified by Houlihan et al. (1986) for use in fish. Fish were not fed 24 h before injection. On the day of injection, six fish from each tank (N = 12 per treatment) were randomly selected, quickly blotted dry, weighed to the nearest 0.01 g, and then injected via the caudal vein with a solution of 150 mM [^{3}H]L-phenylalanine (Sigma, St. Louis, Mo.) containing 37 × 10^6 Bq L-2,6-[^{3}H]phenylalanine·mL^{-1} (Sigma) in Cortland saline (Wolf 1963) at pH 7.5 (injection dose specific activity = 1480 dpm·nmol^{-1}). The dose was 1.0 mL·100 g body weight^{-1} and the fish were not anaesthetized. Following injection, the fish were placed in individual darkened 1-L containers fitted with lids and airlines and containing water taken from the treatment tank from which they had been removed. Approximately 60 min postinjection, fish were killed by a blow to the head and the branchial basket, liver, and a sample of white muscle dorsolateral to the dorsal fin were dissected out and frozen in liquid nitrogen. Individual dissections were completed within 2–4 min. Once frozen, tissues were individually wrapped in aluminum foil, temporarily stored in liquid nitrogen until all fish had been sampled, and then stored at –75°C for later weighing (organ somatic indices) and analysis (protein turnover).

Analysis

Tissue protein and RNA content and fractional rate of protein synthesis were analyzed as detailed in Houlihan et al. (1986). Briefly, tissue samples were homogenized using an electric tissue grinder (IKA A10) in ice-cold 20% perchloric acid (PCA) and the denatured proteins separated by centrifugation. PCA in the supernatant was precipitated with tripotassium citrate and centrifuged, leaving the free phenylalanine in solution. Phenylalanine was converted to β-phenylethylamine by L-tyrosine decarboxylase, extracted using *n*-heptane, and analyzed by a ninhydrin reaction. The content of [^{3}H]phenylalanine was measured using liquid scintillation counting techniques with quench correction. NaOH was used to resuspend the PCA-extracted tissue pellet and duplicate aliquots were taken for analysis of protein content (Lowry et al. 1951). The remaining suspension was acidified with PCA, centrifuged, and the resultant supernatant analyzed for total RNA by the orcinol assay of Munro and Fleck (1966). The pellet, containing protein and DNA, was washed twice with PCA and then hydrolyzed with HCl. Subsequently, the HCl was removed by evaporation. The free amino acids were resuspended in sodium citrate buffer and phenylalanine in the samples determined as described above. The protein synthesis rate (K_s, percent per day) was calculated as

$$K_s = \frac{SA_p}{SA_f} \times \frac{1440}{t} \times 100$$

where SA_p is the protein-bound specific activity (disintegrations per minute per nanomole), SA_f is the specific activity of the pool of free amino acids (disintegrations per minute per nanomole; average measured value 1678.2 ± 174.0, N = 40), 1440 is the number of minutes in a day, t is the exact time (minutes) from the [^{3}H]phenylalanine injection to tissue sampling, and 100 is the conversion to percentage.

The rate of protein degradation (K_d, percent per day) for gill and liver was calculated as the difference between the rate of protein synthesis and the net protein accretion of the tissues (K_g, percent per day), with the latter determined as the product of the average tissue growth rate and average tissue protein content. Specific growth rates were calculated using the equation of Ricker (1979):

$$\text{Growth rate } (K_g, \%\cdot\text{day}^{-1}) = \frac{(\ln W_2 - \ln W_1)}{t} \times 100$$

where W_1 and W_2 are the final and initial weights (grams), respectively, and t is the length of the growing period (days).

This method of estimating protein turnover greatly underestimates protein synthesis rate in white muscle when incorporation times are less than 2 h (Foster et al. 1992). Therefore, white muscle protein synthesis rate must be considered only a relative estimate of protein synthesis in this tissue. Further, it is for this reason that white muscle protein degradation rate could not be calculated.

Liver and gill somatic indices were calculated as the ratio of organ weight to total fish weight, expressed as a percentage of the total, before starting the exposures and at each subsequent sampling period.

As there were differences in the final body weights of the fish, protein synthesis and accretion rates were corrected for body size to a standard 40-g fish (the average weight of the fish following the 90-day exposure) using the log transformation of the allometric equation $Y = aX^b$ and exponents of –0.2 for protein synthesis and –0.41 for protein accretion in accordance with the methods of Houlihan et al. (1986) and Jobling (1983).

Protein synthesis capacity was determined as the ratio of micrograms of tissue RNA to milligrams of tissue protein and tissue translational efficiency of RNA (K_{RNA}, grams protein synthesis per gram RNA per day) calculated by dividing the protein synthesis capacity by the appropriate fractional rate of protein synthesis value multiplied by 10 (Sugden and Fuller 1991).

Statistical analysis

Values shown in figures are means ± 1 standard error of the mean (SE). Statistical differences between treatment means on a specific day were determined by analysis of variance (ANOVA) followed by Fisher's LSD multiple comparison test, using a commercial statistical software package (Statview 512+); 95% was accepted as the level of confidence.

Results

Organ somatic indices

Before exposure, the branchial baskets and liver of the hardwater-acclimated trout represented approximately 2.8 and 1.4% of the total body weight, respectively (Fig. 2). Values tended to decline slightly during the exposures, but none of the treatment effects were statistically significant. Thus, organ somatic indices were not sensitive indicators of the organ-specific impact of combinations of chronic exposure to elevated environmental temperature and water total ammonia.

Protein turnover: gill

Before exposure, gills of these hardwater-acclimated fish

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Fig. 2. Effect of water temperature and total ammonia level on the (A) branchial basket and (B) liver somatic indicies of hardwater-acclimated fish. The organ somatic indicies were measured before exposure (day 0) and at 30, 60, and 90 days of exposure. Solid histograms, control water temperature and ambient total ammonia (6.0 μmol·L^{-1}); angled hatched histograms, base water temperature with elevated total ammonia (70 μmol·L^{-1}); open histograms, ambient total ammonia at base+2°C; horizontally hatched histograms, base+2°C water with elevated total ammonia. Data are presented as means ± 1 SE (N = 12).

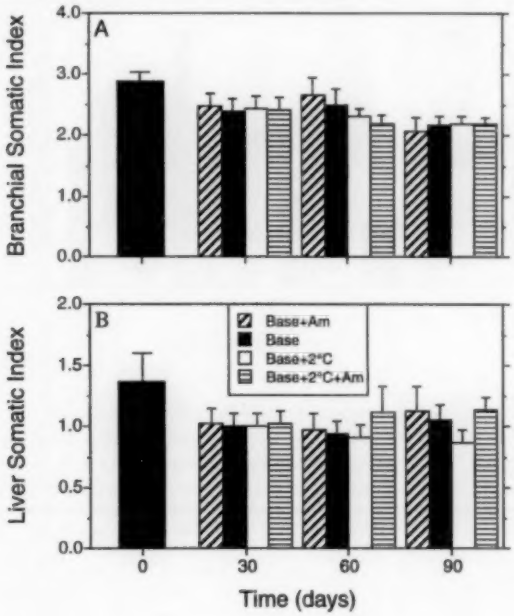
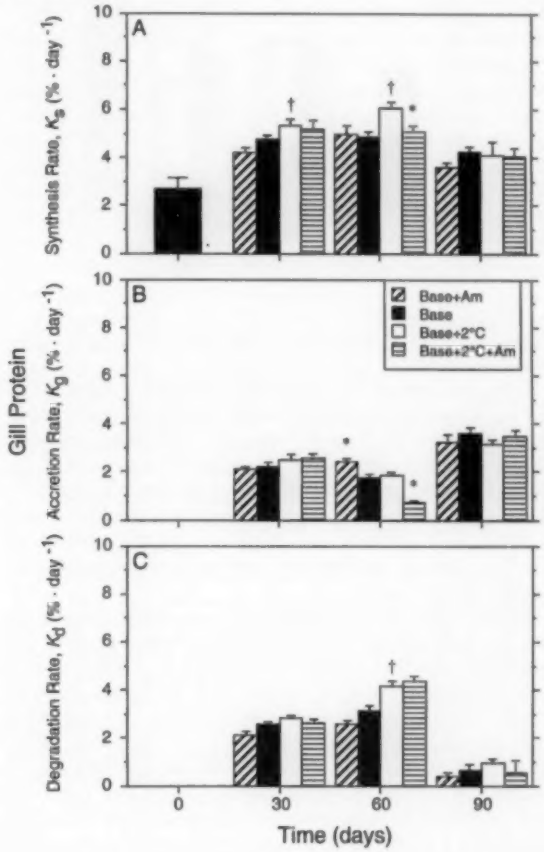


Fig. 3. Effect of water temperature and total ammonia level on gill protein (A) synthesis, (B) accretion, and (C) degradation rates in hardwater-acclimated trout. All rates were calculated on a %·day^{-1} basis and determined as outlined in Materials and methods. Data are presented as outlined in Fig. 2. Protein synthesis and accretion rates were corrected to a standard body size of 40 g (see Materials and methods for details). An asterisk indicates a statistically significant difference (P < 0.05) between the two levels of total ammonia (6.0 versus 70 μmol·L^{-1}) at the same temperature and a dagger indicates a significant difference (P < 0.05) between temperature groups at the ambient water ammonia concentration (6.0 μmol·L^{-1}).



synthesized proteins at a body size corrected rate of approximately 3%·day^{-1} (Fig. 3A). Rates increased to about 5%·day^{-1} at days 30 and 60 but fell again to about 3.5%·day^{-1} at day 90. The addition of 2°C (base+2°C) was found to influence gill protein synthesis of hardwater-acclimated trout to a greater extent than was observed in softwater-acclimated trout exposed under nearly identical conditions (Reid et al. 1997*a*). At both days 30 and 60, gill protein synthesis was greater in the base+2°C group than in the base temperature group. Also, there is some evidence to suggest that exposure to elevated total ammonia may have inhibited gill protein synthesis. However, only at day 60 and within the higher temperature treatment groups did elevated total ammonia significantly reduce gill protein synthesis. In general, it appears that ammonia had less effect on protein synthesis in this tissue than did exposure of softwater-acclimated juvenile rainbow trout to pH 5.2 under similar conditions (Reid et al. 1997*a*).

No significant influence of water temperature and ammonia on net gill protein accretion was obvious at either day 30 or 90 (Fig. 3B), although some differences were statistically significant at day 60. At this time, protein accretion rates in gills from fish at base temperature were significantly enhanced at elevated total ammonia, while the opposite response was observed at the higher water temperature (base+2°C), despite the fact that, alone, water temperature appeared to have no influence on gill protein accretion rate at this time. Interestingly, these effects at day 60 were similar to those changes in responses to temperature and pH in gills from softwater-acclimated fish at the same time (Reid et al. 1997*a*).

Protein degradation rates in gills of hardwater-acclimated fish tended to reflect changes in protein synthesis in response to elevated water temperature and total ammonia (Fig. 3C). Exposure to elevated water temperature tended to enhance rates of protein degradation, while in five of six cases, exposure to elevated total ammonia suppressed the rate at which proteins were broken down, although the differences were not statistically significant. Note the large suppression of protein

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Fig. 4. Effect of water temperature and total ammonia level on gill protein content. All values were calculated on a percent basis (mg protein·mg sample^{-1} × 100%) and were determined as outlined in Materials and methods. Data are presented as outlined in Fig. 2 and statistically evaluated as in Fig. 3.

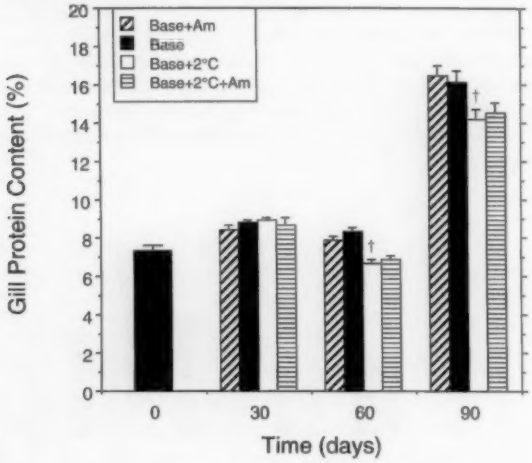
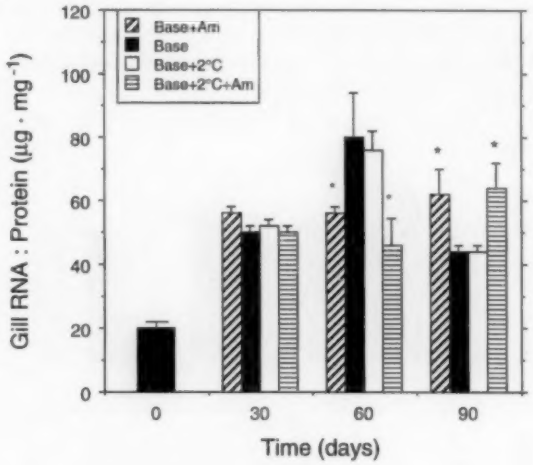


Fig. 5. Effect of total ammonia and water temperature on gill RNA:protein. The RNA:protein values (tissue protein synthesis capacity) were calculated and expressed as mg RNA·mg protein^{-1} and were determined as outlined in Materials and methods. Data are presented as outlined in Fig. 2 and statistically evaluated as in Fig. 3.



degradation rates at day 90 in all groups, shortly after peak water temperatures.

Before the start of the experiment, gill protein content was 7.4 ± 0.3% (milligrams of protein per 100 mg of tissue, Fig. 4). During the first 60 days of exposure, gill protein content changed very little, although it was slightly suppressed in the base+2°C groups at day 60. However, the mean gill protein content of all treatment groups approximately doubled at day 90, again with evidence of suppression by the addition of 2°C. There was no apparent influence of elevated water total ammonia at any time.

Gill protein synthesis capacity (RNA:protein), initially 20 ± 2.1 µg RNA·mg protein^{-1}, increased approximately 2.5 times during the first 30 days of exposure as a result of dramatic increases in gill RNA content (Fig. 5). This increase in gill RNA, relative to gill protein, resulted in a 27% reduction in gill translational efficiency (Table 1). No treatment effect was evident at this time. However, during the subsequent 30 days, the protein synthesis capacity in gills of fish held under conditions of ambient water total ammonia increased an additional 1.5 times. RNA:protein values in the gills of fish exposed to elevated water total ammonia were significantly lower than in their respective controls, and the gill protein synthesis capacity in these fish was not different from day 30 values. At the same time, gill translational efficiencies in fish exposed to the elevated water ammonia concentration tended to be greater than in the appropriate controls (Table 1).

During the final 30 days, the period of peak water temperatures, dramatic increases in gill protein content were noted. Despite the near doubling of gill protein content over this period, values for fish exposed to base+2°C water remained significantly lower than for the ambient fish. The gill protein synthesis capacity of the base and base+2°C fish dropped dramatically from the day 60 values, while, similar to the previous 30 days of exposure, little change was evident in the gill RNA:protein of those fish exposed to 70 µmol total ammonia·L^{-1}. The result was that at day 90, the gill protein synthesis capacities of fish exposed to elevated ammonia were significantly greater than in their respective controls. Despite this, gill translational efficiencies were significantly lower in the 70 µmol total ammonia·L^{-1} fish than in the appropriate controls (Table 1).

Table 1. Branchial ribosomal translational efficiency (K_{RNA}, g protein synthesis·g RNA^{-1}·day^{-1}) from juvenile rainbow trout chronically exposed to elevated water total ammonia (Am, 70 µmol·L^{-1}) and an elevated seasonal temperature profile (+2°C).

	Time			
Exposure group	Day 0	Day 30	Day 60	Day 90
Base+Am		0.86±0.09	0.88±0.06	0.58±0.15*
Base	1.33±0.23	0.95±0.07	0.61±0.18	0.97±0.08
Base+2°C		1.03±0.07	0.79±0.12	0.94±0.08
Base+2°C+Am		1.04±0.08	1.11±0.60	0.63±0.14*

Note: Values are the means ± SE with a sample size of 12 for each group. Ribosomal translational efficiency was calculated from the RNA:protein (Fig. 5) and the fractional rate of protein synthesis (Fig. 3).

*Statistically significant difference ($P < 0.05$) between the two levels of water total ammonia at the same temperature.

Protein turnover: liver

Protein synthesis in the livers of hardwater-acclimated juvenile trout were similar to those of softwater-acclimated fish (Reid et al. 1997*a*) at approximately 3%·day^{-1} before their exposure to the treatment regime (Fig. 6A). Liver protein dynamics were more consistent than those of the gills in their response to chronic exposure to elevated total ammonia and additional temperature. At day 30, there was little influence of treatment on liver protein synthesis. After 60 days of exposure, protein synthesis was significantly increased in response to chronic elevations in total ammonia by approximately 65 and

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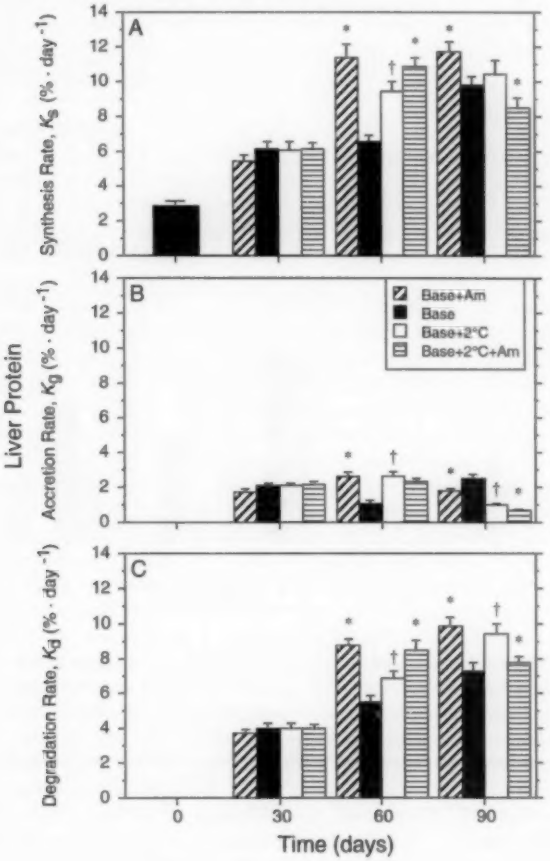
Fig. 6. Effect of water temperature and total ammonia level on liver protein (A) synthesis, (B) accretion, and (C) degradation rates in hardwater-acclimated trout. All rates were calculated on a %·day^{-1} basis and determined as outlined in Materials and methods. Data are presented, body size corrected, and statistically evaluated as outlined in Figs. 2 and 3, respectively.



40% at base and base+2°C temperatures, respectively. In addition, liver protein synthesis was significantly enhanced by the addition of 2°C to the base temperature at ambient levels of water total ammonia. At day 90, protein synthesis in the base temperature group remained significantly enhanced in the presence of elevated total ammonia (base+Am). However, it appeared that the high water temperatures experienced by the base+2°C fish at this time resulted in a reduction in protein synthesis because there was no longer any significant enhancement in protein synthesis as a result of the additional temperature or total ammonia. Furthermore, elevated total ammonia during this time resulted in a significant inhibition of liver protein synthesis in fish at the higher water temperature (base+2°C+Am), a result opposite to that in fish at ambient water temperature (base+Am).

Liver protein accretion was insensitive to alterations in water temperature and total ammonia levels during the first 30 days of exposure (Fig. 6B). At day 60, however, water temperature and total ammonia levels induced alterations in protein accretion similar to the observed changes in protein synthesis (Fig. 6A). Both the 2°C elevation in water temperature at ambient ammonia levels and increased total ammonia at the ambient water temperature significantly enhanced net accumulation of protein in the liver. By day 90, however, the stimulatory influence of both temperature and ammonia had been lost. In fact, both the increase in water temperature and the increases in total ammonia inhibited, rather than enhanced, liver protein accretion.

Liver protein degradation rates tended to reflect changes in protein synthesis in response to elevated water temperature and total ammonia. Exposure to elevated water temperature resulted in significantly greater protein degradation at both days 60 and 90 (Fig. 6C). At day 60, exposure to elevated total ammonia also significantly enhanced the rate at which liver proteins were broken down at both temperatures. During the final 30 days, exposure to elevated total ammonia significantly altered liver protein degradation, but in opposite ways depending on temperature. At the ambient temperature, the additional ammonia stimulated protein degradation. However, during this period of peak ambient water temperature and in the base+2°C treatment group, the elevated total ammonia (base+2°C+Am) resulted in a significant reduction in protein degradation.

Before the start of the experiment, liver protein content was 23.4 ± 2.8% (milligrams of protein per 100 mg of tissue) with little change throughout the 90-day exposure. At the 60-day period, liver protein content was reduced 8% in fish exposed to 70 μmol total ammonia·L^{-1} at the base temperature and 14% when exposed at the base+2°C temperature. At day 90 of the exposure, liver protein content of the base+2°C+Am fish was significantly greater than in their respective controls (base+2°C), 27.5 ± 0.5 and 24.5 ± 0.7 mg protein·100 mg tissue^{-1}, respectively.

The liver protein synthesis capacity (RNA:protein), initially 40 ± 6 μg RNA·mg protein^{-1}, increased gradually over the first 60 days of exposure to reach a peak of 100 μg RNA·mg protein^{-1} in the base+2°C treatment group (Fig. 7). No treatment effects were evident during this period of the exposure. Following the period of peak environmental temperatures, days 60–90, liver protein synthesis capacities in all treatment groups tended to fall. Although an influence of elevated water ammonia on liver protein synthesis capacity was not evident, the addition of +2°C caused a significant inhibition.

Liver ribosomal translational efficiency was 0.71 ± 0.13 g protein·g RNA^{-1}·day^{-1} before the start of the exposures (Table 2). At day 30, liver translational efficiency in all groups increased by an average of 35% as a result of the near doubling of protein synthesis (Fig. 6A) and an approximate 50% increase in RNA:protein (Fig. 7) in the liver. However, no treatment effect was apparent at this time. This modification in ribosomal translational efficiency was again observed during the following 30-day period. However, at day 60, a treatment effect was apparent, as the ribosomal translational efficiency of trout exposed to elevated total ammonia at the ambient temperature (base+Am) was significantly greater than that in the base temperature, ambient total ammonia fish. During the final 30 days of the experiment, ribosomal translational efficiency increased in all treatment groups, as was observed for the previous two sampling periods (Table 2). The increase in

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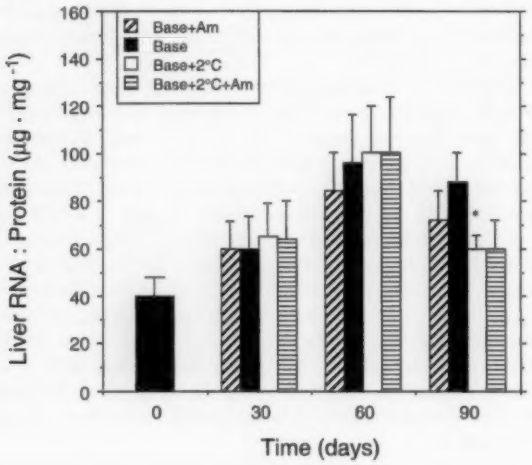
Fig. 7. Effect of total ammonia and water temperature on liver RNA:protein. The RNA:protein values (tissue protein synthesis capacity) were calculated and expressed as μg RNA·mg protein^{-1} and were determined as outlined in Materials and methods. Data are presented as outlined in Fig. 2 and statistically evaluated as in Fig. 3.



ribosomal translational efficiency at day 90 was attributed to the overall decrease in liver protein synthesis capacity (Fig. 7) more so than to any change in liver protein synthesis (Fig. 6A). As was observed at day 30, no treatment effect was apparent at this time.

Protein turnover: white muscle

White muscle protein synthesis declined over time in all treatment groups but was not influenced by chronic exposure to elevated total ammonia or temperature (Fig. 8A).

White muscle protein accretion in hardwater-acclimated fish was also unaffected by treatment during the first month of exposure (Fig. 8B). During the second month, protein accretion was significantly greater in both elevated ammonia (at ambient water temperature; base+Am) and elevated temperature treatments due to an apparent reduction in the white muscle protein accretion rate in fish exposed to the base temperature treatment and ambient total ammonia (base). At day 90, the net accumulation of protein in this tissue was affected in a manner nearly identical to that observed during this period in this tissue of softwater-acclimated fish exposed for 90 days to combinations of water temperature and pH (Reid et al. 1997*a*). At base temperature, elevated total ammonia (base+Am) inhibited protein accretion, as did the elevation in water temperature (at ambient total ammonia; base). As mentioned in the Materials and methods section, white muscle degradation rates could not be calculated because of the short incorporation times for phenylalanine with respect to this tissue.

White muscle protein content (11.8 ± 0.7%) was not influenced by water temperature or total ammonia over the duration of the 90-day experiment. RNA content was similarly unaffected which resulted in a relatively unaltered RNA:protein of 6.0 ± 0.3 μg RNA·mg protein^{-1}. Thus, white muscle translational efficiency simply reflected the changes in protein synthesis over the duration of the exposure (data not shown).

Fig. 8. Effect of water temperature and total ammonia level on white muscle protein (A) synthesis and (B) accretion rates in hardwater-acclimated trout. All rates were calculated on a %·day^{-1} basis and determined as outlined in Materials and methods. Data are presented, body size corrected, and statistically evaluated as outlined in Figs. 2 and 3, respectively.

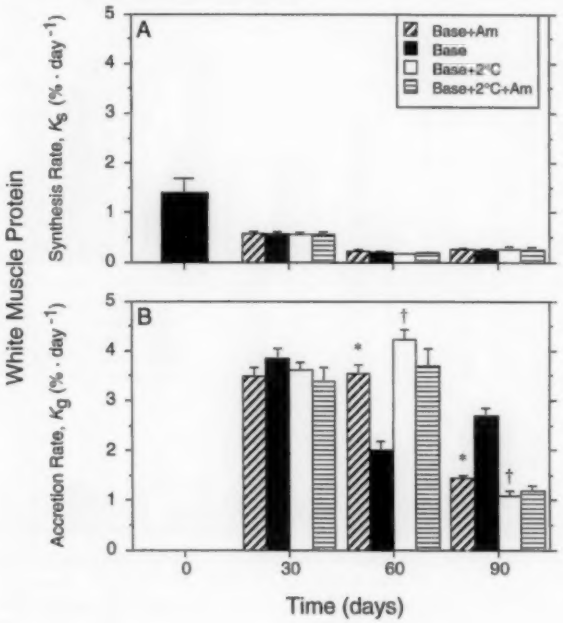


Table 2. Liver ribosomal translational efficiency (K_{RNA}, g protein synthesis·g RNA^{-1}·day^{-1}) from juvenile rainbow trout chronically exposed to elevated water total ammonia (Am, 70 μmol·L^{-1}) and an elevated seasonal temperature profile (+2°C).

	Time			
Exposure group	Day 0	Day 30	Day 60	Day 90
Base+Am		0.91±0.17	1.35±0.26*	1.62±0.27
Base	0.71±0.13	1.02±0.24	0.68±0.12	1.11±0.15
Base+2°C		0.94±0.20	0.93±0.18	1.73±0.24
Base+2°C+Am		0.96±0.24	1.08±0.25	1.41±0.29

Note: Values are the means ± SE with a sample size of 12 for each group. Ribosomal translational efficiency was calculated from the RNA:protein (Fig. 7) and the fractional rate of protein synthesis (Fig. 6).

*Statistically significant difference ($P < 0.05$) between the two levels of water total ammonia at the same temperature.

Discussion

In the past, tissue protein turnover rates have been used successfully to provide general estimates of the costs associated with acute or chronic sublethal exposure to stressors such as waterborne metals (Zn: Hogstrand et al. 1995; Al: Wilson et al. 1996*a*), sewage sludge (Houlihan et al. 1994), temperature (Goolish et al. 1984; Fauconneau and Arnal 1985; Loughna and Goldspink 1985; Foster et al. 1992), and environmental

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acidification (Wilson et al. 1996*a*; Reid et al. 1997*a*). The application of the protein synthesis assay to the present experimental design, the factors that influence it, the limitations of the assay, the interpretation of metabolic cost based on changes in protein turnover, and the unique features of the current approach have been discussed elsewhere (Reid et al. 1995, 1997*a*, 1997*b*). In the companion study (Reid et al. 1997*a*), fish were similarly exposed to two temperature profiles separated by approximately 2°C, but in the presence and absence of low water pH in softwater.

Temperature

Due to the direct link between the environmental temperature and the metabolic rate in ectotherms, it might be predicted that chronic exposure to a slightly warmer environment (i.e., +2°C) would enhance protein synthesis in fish. This is clearly the case when exposure temperatures have differed considerably more than in the present study (Δ8°C: Fauconneau and Arnal 1985; Δ15°C: Loughna and Goldspink 1985). In addition to the much larger differences in temperature, these and most similar studies have used fish that are acclimated and exposed to constant temperature. Not only was the temperature difference between our control (base) and +2°C fish quite small, this difference was superimposed upon a temperature profile that incorporates much of the natural daily and seasonal temperature variation that would be associated with the inshore region of Lake Ontario. Nonetheless, despite these unique characteristics of this and the similarly designed companion study (Dockray et al. 1996; Reid et al. 1997*a*), we demonstrated numerous physiological responses to chronic exposure to a slightly warmer environment, including changes in tissue protein turnover, the absolute sum of protein synthesis and protein degradation.

In this study, gill and liver protein turnover increased by an overall average of 18.4% as a result of exposure to water temperature only 2°C above the base temperature, with the largest change in protein turnover occurring between days 30 and 60. Protein turnover has been shown to be directly proportional to ration size (Houlihan et al. 1988, 1995); however, there was no difference in the food intake between these two groups (Linton et al. 1997). These findings are similar to the increase in gill and liver protein turnover that occurred when similarly acclimated juvenile rainbow trout were exposed to a 2.0 ± 0.2°C elevation in the winter temperature profile in our laboratory system (Morgan et al. 1998). These authors found that gill and liver protein turnover increased by an average of 20.5% as a result of the 2°C increase in water temperature during the months of January–April. Furthermore, when softwater-acclimated juvenile rainbow trout were exposed to a nearly identical temperature profile during both the summer (Reid et al. 1997*a*) and winter months (Morgan et al. 1998), gill and liver protein turnover increased by an average of 10 and 12.2%, respectively. Taken together, these findings support our earlier suggestion (Reid et al. 1995) that the decreased responsiveness of protein turnover in fish in softwater to an identical elevation in the normal temperature profiles might be attributed to the inherently greater metabolic cost associated with living in an ion-poor environment.

The mechanism through which the 2°C elevation in the base temperature profile increased protein turnover appears to have been an increase in ribosomal translational efficiency. Although not statistically significant, in 75% of the comparisons (not including day 90 rates which followed the high temperature shock), the ribosomal translational efficiencies in gill and liver were higher at the +2°C temperature than at the base water temperature (Tables 1 and 2). The rationale for not including the day 90 rates was that during this time, when the ambient temperature had recently approached nearly lethal temperatures for rainbow trout (Kaya 1978), there was a significant change in liver protein synthesis capacity (Fig. 7). Despite the influence of this period of extreme base water temperature, our findings are consistent with other studies in which elevated water temperature also stimulated protein synthesis via increases in tissue ribosomal translational efficiency with little or no change in tissue protein synthesis capacity (Goolish et al. 1984; Fauconneau and Arnal 1985; Morgan et al. 1998).

Ammonia

Ammonia is largely formed in the liver and requires no modification and therefore little energy for excretion. In contrast, urea synthesis and excretion consumes energy (Wood 1993). Urea excretion was unaffected by chronic sublethal ammonia exposure at base or base+2°C (Linton et al. 1997). However, total nitrogenous waste excretion, and therefore ammonia excretion, tended to be highest in fish exposed to elevations in water ammonia during the first 60 days of this exposure (Linton et al. 1997). Plasma ammonia levels in hardwater-acclimated fish were unaffected by 30 days of exposure to 70 μM total ammonia·L^{-1} at either temperature. However, during the subsequent 60 days, plasma ammonia levels in fish chronically exposed to elevated ammonia (base+Am) were significantly greater than in those exposed to only ambient concentrations of water total ammonia at the base temperature. Similar, although not statistically significant, alterations in plasma ammonia in ammonia-exposed fish were apparent at the base+2°C temperature at days 60 and 90 (Linton et al. 1997).

This period of elevated plasma ammonia levels corresponds to the dramatic enhancement in liver protein synthesis and degradation measured at day 90 in both the base and base+2°C treatment groups (Fig. 6). As any detoxification of plasma ammonia would involve the liver and glutamine synthetase (Wood 1993), our data indicate that these changes in liver protein turnover may have been stimulated by this period of elevated plasma ammonia and that this is a response directed at reestablishing more normal levels of plasma ammonia. Furthermore, the stimulation of protein turnover in the liver by elevated water ammonia may provide the explanation for the stimulation of growth, nitrogen and energy conversion, and higher nitrogen retention efficiency reported by Linton et al. (1997). The additional plasma ammonia load, once incorporated into glutamine (Wood 1993) and other amino acids, could be used as substrates for protein synthesis. Thus, this ammonia-based increase in available amino acids could result in the apparent increase in food conversion efficiency, nitrogen retention, and enhanced growth in the absence of any apparent increase in food consumption (Linton et al. 1997).

There was some evidence to suggest that gill protein turnover, primarily degradation, was reduced by chronic exposure to elevated ammonia (Fig. 3). The apparent reductions in protein degradation may have been sufficient to maintain or marginally enhance net protein accretion in this tissue. Interestingly, similar alterations in protein turnover were

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observed in the gills of softwater-acclimated fish exposed to sublethal acidity (Reid et al. 1997*a*). The majority of nitrogenous wastes is excreted across the gills (Sayer and Davenport 1987), and this organ is also the likely tissue across which ammonia would enter the animal. Elevated water ammonia concentration might be expected to impair branchial ionoregulation through inhibition of Na^+ uptake (Wilson et al. 1996*b*) with the compensatory response being the production of additional enzymes or new Na^+ channels. Indeed, measurements of Na^+ unidirectional fluxes revealed that the fish chronically exposed to elevated total ammonia exhibited higher rates of Na^+ turnover (Linton et al. 1998). Perhaps the enhanced net protein accretion in the gills was in some way associated with this greater Na^+ transport capacity.

The mechanism by which sublethal ammonia influenced protein turnover appears to involve alterations in both tissue protein synthesis capacity and ribosomal translational efficiency, depending on the tissue and duration of the exposure at sampling. Despite only minor changes in gill protein synthesis, degradation, and accretion during the last 60 days of the exposure, the data do suggest that chronic exposure to elevated total ammonia altered gill protein synthesis capacity (Fig. 5). As a consequence, normal levels of protein turnover appear to have been maintained through compensatory adjustments in gill ribosomal translational efficiency (Table 1). However, in the liver, where significant alterations in protein turnover were observed, the elevation in protein turnover induced by ammonia resulted from enhanced ribosomal translational efficiency (Table 2). Liver protein synthesis capacity was unaffected by chronic exposure to sublethal total ammonia (Fig. 7). Evidence that protein turnover in gill and liver is affected by environmental stressors through different mechanisms has been reported previously by us, in response to chronic exposure to a low-pH environment (Reid et al. 1997*a*).

Other possible mechanisms have been suggested that may be independent of changes in protein synthesis capacity or translational efficiency. Houlihan et al. (1994) chronically exposed dab (*Limanda limanda*) to a mixture of metals contained within sewage sludge and determined monthly rates of tissue protein turnover (white muscle, liver, kidney, and spleen) using methods similar to those of the present study. Despite no impact on tissue protein synthesis, protein growth rates (accretion) were lower in fish chronically exposed to sewage sludge compared with the control group. Houlihan et al. (1994) suggested that chronic exposure to sewage sludge reduced protein accretion through enhanced protein degradation, as tissue RNA concentrations and posttranslational efficiency were largely unaffected. Similarly, Wilson et al. (1996*a*) reported no significant modification in protein synthesis capacity or ribosomal translational efficiency in gill, liver, and carcass (whole body minus gills and liver) following 15 days of exposure to pH 5.2 softwater when compared with the pH 6.5 controls. However, in response to the addition of 30 $\mu g\ Al \cdot L^{-1}$, these authors noted a significant reduction in gill protein synthesis capacity and a significant reduction in carcass ribosomal translational efficiency, with no impact on either parameter in liver following a 32-day exposure. Thus, in response to chronic stressors, it appears that there are no common mechanisms responsible for alterations in tissue protein turnover. It seems possible that modifications in protein turnover can result from pre- or post-translational modification of protein synthesis, alterations in protein degradation, or both and may differ between tissues within the same individual.

Ammonia and temperature

The impact of this combination of stressors on gill protein turnover was negligible, as the impact of ammonia was neither enhanced nor suppressed as the result of the 2°C elevation in the base temperature profile. In the case of the liver, however, our findings suggest that the combination of elevated temperature and ammonia results in a reduction in the stimulator influence that each has separately on liver protein turnover (Fig. 6). This was evident at both days 60 and 90 of the experiment, with the combination effect being more dramatic at day 90, presumably due to the high ambient temperature (Fig. 1). Linton et al. (1997) drew similar conclusions as to the impact of the combination of elevated temperature and total ammonia based on a suite of quantitative bioenergetic and physiological measurements made on fish exposed to the exact same conditions during the same season of the year. Nonetheless, these finding are somewhat contrary to those of the companion low-pH softwater study (Reid et al. 1997*a*). In that study, we reported that the impacts of the addition of 2°C to the base temperature profile and of the environmental acidification were, in the gills of softwater-acclimated trout, additive. Therefore, we suggest that the physiological impact of a warmer and polluted environment will depend on the site and mechanism of action of the pollutant of concern and whether the fish are in ion-poor or ion-rich water. However, when water temperatures approach the upper lethal temperature for a given species of fish, the additional 2°C would triggered a dramatic reduction in tissue protein turnover and thereby mask any influence of a pollutant on protein turnover.

Summary

The present study has shown that protein turnover rates in the tissues of fish exposed chronically to sublethal levels of total ammonia are altered in a manner consistent with the hepatic detoxification of accumulated internal ammonia. When chronically exposed to elevated total ammonia, liver protein turnover was enhanced, while the rates in the gill were not affected. The addition of +2°C to the environment generally increased protein synthesis in both the gills and liver; however, in combination with exposure to sublethal levels of total ammonia the ammonia-stimulated increase in protein turnover was muted. The dominant impact of the 2°C elevation was most apparent during the last 30 days of the experiment when ambient summer water temperature peaked several times at 22°C. Therefore, even if the rise in mean global temperature triggered by the doubling of atmospheric CO_2 is in the lower part of the overall range (0.5–7°C) predicted by current models, the results of this study suggest that it would increase the cost of living for fish already exposed to elevated water ammonia concentrations. The consequences of such changes in the quality of the aquatic environment would be particularly severe if these animals are living near the upper limit of their temperature tolerance.

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References

Calow, P. 1991. Physiological costs of combating chemical toxicants: ecological implications. Comp. Biochem. Physiol. C Comp. Pharmacol. **100**: 3–6.

DeAngelis, D.L., and R.M. Cushman. 1990. Potential application of models in forecasting effects of climate changes on fisheries. Trans. Am. Fish. Soc. **119**: 224–239.

Dockray, J.J., Reid, S.D., and Wood, C.M. 1996. Effects of elevated summer temperatures and reduced pH on metabolism and growth of juvenile rainbow trout (*Oncorhynchus mykiss*) on unlimited ration. Can. J. Fish. Aquat. Sci. **53**: 2752–2763.

Fauconneau, B., and Arnal, M. 1985. *In vivo* protein synthesis in different tissues and the whole body of rainbow trout (*Salmo gairdneri* R.). Influence of environmental temperature. Comp. Biochem. Physiol. A Comp. Physiol. **82**: 179–187.

Foster, A.R., Houlihan, D.F., Hall, S.J., and Burren, L.J. 1992. The effects of temperature acclimation on protein synthesis rates and nucleic acid content of juvenile cod (*Gadus morhua* L.). Can. J. Zool. **70**: 2095–2102.

Garlick, P.J., McNurlan, M.A., and Preedy, V.R. 1980. A rapid and convenient technique for measuring the rate of protein synthesis in tissues by injection of [^{3}H]phenylalanine. Biochem. J. **192**: 719–723.

Goolish, E.M., Barron, M.G., and Adelman, I.R. 1984. Thermoacclimatory response of nucleic acid and protein content of carp muscle tissue: influence of growth rate and relationship to glycine uptake by scales. Can. J. Zool. **62**: 2164–2170.

Hogstrand, C., Reid, S.D., and Wood, C.M. 1995. Calcium versus zinc transport in the gills of freshwater rainbow trout, and the cost of adaptation to waterborne zinc. J. Exp. Biol. **198**: 337–348.

Houlihan, D.F. 1991. Protein turnover in ectotherms and its relation to energetics. *In* Advances in comparative and environmental physiology. Vol. 7. *Edited by* R. Gilles. Springer-Verlag, Berlin. pp. 1–44.

Houlihan, D.F., McMillan, D.N., and Laurent, P. 1986. Growth rates, protein synthesis, and protein degradation rates in rainbow trout: effect of body size. Physiol. Zool. **59**: 482–493.

Houlihan, D.F., Hall, S.J., Gray, C., and Noble, B.S. 1988. Growth rates and protein turnover in Atlantic cod, *Gadius morhua*. Can. J. Fish. Aquat. Sci. **45**: 951–964.

Houlihan, D.F., Costello, M.J., Secombes, C.J., Stagg, R., and Brechin, J. 1994. Effects of sewage sludge exposure on growth, feeding and protein synthesis of dab (*Limanda limanda* (L.)). Mar. Environ. Res. **37**: 331–353.

Houlihan, D.F., Pedersen, B.H., Steffensen, J.F., and Brechin, J. 1995. Protein synthesis, growth and energetics in larval herring (*Clupea harengus*) at different feeding regimes. Fish Physiol. Biochem. **14**: 195–208.

Jobling, M. 1983. Growth studies with fish — overcoming the problems of size variation. J. Fish Biol. **22**: 153–157.

Jobling, M. 1985. Growth. *In* Fish energetics: new perspectives. *Edited by* P. Tytler and P. Calow. Croom Helm, London, U.K. pp. 213–230.

Kaya, C.M. 1978. Thermal resistance of rainbow trout from a permenantly heated stream, and of two hatchery strains. Prog. Fish-Cult. **40**: 138–142.

Linton, T.K., Reid, S.D., and Wood, C.M. 1997. The metabolic costs and physiological consequences to juvenile rainbow trout of a simulated summer global warming regime in the presence and absence of sublethal ammonia. Trans. Am. Fish. Soc. **126**: 259–272.

Linton, T.K., Morgan, I.J., Reid, S.D., and Wood, C.M. 1998. Long term exposure to small temperature increase and sublethal ammonia: does acclimation occur? Aquat. Toxicol. **40**: 171–191.

Loughna, P.T., and Goldspink, G. 1985. Muscle protein synthesis rates during temperature acclimation in euryhaline (*Cyprinus carpio*) and a stenothermal (*Salmo gairdneri*) species of teleost. J. Exp. Biol. **118**: 267–276.

Lowry, O.H., Rosebrough, N.J., Farr, A.L., and Randall, R.J. 1951. Protein measurement with the Folin reagent. J. Biol. Chem. **193**: 265–275.

Mohnen, V.A., and Wang, W.-C. 1992. An overview of global warming. Environ. Toxicol. Chem. **11**: 1051–1059.

Morgan, I.J., D'Cruz, L.M., Dockray, J.J., Linton, T.K., McDonald, D.G., and Wood, C.M. 1998. The effects of elevated winter temperature and sublethal pollutants (low pH, elevated ammonia) on protein turnover in the gill and liver of rainbow trout (*Oncorhynchus mykiss*). Fish Physiol. Biochem. In press.

Munro, H.N., and Fleck, A. 1966. The determination of nucleic acids. *In* Methods of biomedical analysis. Vol. XIV. *Edited by* D. Glick. Interscience, New York. pp. 113–176.

Regier, H.A., Holmes, J.A., and Pauly, D. 1990. Influence of temperature changes on aquatic ecosystems: interpretation of empirical data. Trans. Am. Fish. Soc. **119**: 374–389.

Reid, S.D., Dockray, J.J., Linton, T.K., McDonald, D.G., and Wood, C.M. 1995. Effects of a summer temperature regime representative of a global warming scenario on growth and protein synthesis in hardwater- and softwater-acclimated juvenile rainbow trout (*Oncorhynchus mykiss*). J. Therm. Biol. **20**: 231–244.

Reid, S.D., Dockray, J.J., Linton, T.K., McDonald, D.G., and Wood, C.M. 1997*a*. Effects of chronic environmental acidification and a summer global warming scenario: protein synthesis in juvenile rainbow trout (*Oncorhynchus mykiss*). Can. J. Fish. Aquat. Sci. **54**: 2014–2024.

Reid, S.D., McDonald, D.G., and Wood, C.M. 1997*b*. Interactive effects of temperature and pollutant stress. *In* Global warming: Implications for freshwater and marine fish. *Edited by* D.G. McDonald and C.M. Wood. Society for Experimental Biology Seminar Series 61. Cambridge University Press, Cambridge, U.K. pp. 325–350.

Ricker, W.E. 1979. Growth rates and models. *In* Fish physiology. Vol. 8. *Edited by* W.S. Hoar, D.J. Randall, and J.R. Brett. Academic Press, New York. pp. 677–742.

Sayer, M.D.J., and Davenport, J. 1987. The relative importance of the gills to ammonia and urea excretion in five seawater and one freshwater teleost species. J. Fish Biol. **31**: 561–570.

Schindler, D.W., Beaty, K.G., Fee, E.J., Cruikshank, D.R., Debruyn, E.R., Findlay, D.L., Shearer, J.A., and Turner, M.A. 1990. Effects of climatic warming on lakes of the central boreal forest. Science (Washington, D.C.), **250**: 967–970.

Sugden, P.H., and Fuller, S.J. 1991. Regulation of protein turnover in skeletal and cardiac muscle. Biochem. J. **273**: 21–37.

Verdouw, H., van Echted, C.J.A., and Dekkers, E.M.J. 1978. Ammonia determination based on indophenol formation with sodium salicylate. Water Res. **12**: 399–402.

Wilson, R.W., Wood, C.M., and Houlihan, D.F. 1996*a*. Growth and protein turnover during acclimation to acid and aluminum in juvenile rainbow trout (*Oncorhynchus mykiss*). Can. J. Fish. Aquat. Sci. **53**: 802–811.

Wilson, R.W., Wright, P.M., Munger, S., and Wood, C.M. 1996*b*. Ammonia excretion in freshwater rainbow trout (*Oncorhynchus*

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mykiss) and the importance of gill boundary layer acidification: lack of evidence for Na^+/NH_4^+ exchange. J. Exp. Biol. **191**: 37–58.

Wolf, K. 1963. Physiological salines for freshwater teleosts. Prog. Fish-Cult. **25**: 135–140.

Wood, C.M. 1993. Ammonia and urea metabolism and excretion. *In* The physiology of fishes. *Edited by* D.H. Evans. CRC Press, Baton Rouge, Fla. pp. 379–424.

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PERSPECTIVE

Recent international agreements and the precautionary approach: new directions for fisheries management science

Laura J. Richards and Jean-Jacques Maguire

Abstract: The dynamics of exploited fish populations can be highly uncertain and the precautionary approach to fisheries management addresses such uncertainties. The precautionary approach is now embodied in several international agreements, including (*i*) the UN Straddling Fish Stocks and Highly Migratory Fish Stocks Agreement and (*ii*) the FAO Code of Conduct. We discuss how application of these agreements will change the daily operations of many fisheries agencies. Contrary to past practices, the absence of adequate scientific information can no longer be a reason for postponing or failing to take conservation measures. Future harvest strategies will be based on stock-specific reference points and predefined decision rules. However, more research is required to quantify uncertainties associated with reference point definitions and their practical application in a management context. In addition, future research will emphasize environmental issues with extensive data requirements, such as ecosystem impacts of fishing. Data collection will remain a core business activity; agencies must address the costs of maintaining shared and documented data archives over the long term.

Résumé : La dynamique des populations de poissons exploitées peut être très incertaine, et la gestion des pêches selon l'approche de précaution prend en compte ces incertitudes. Cette stratégie est maintenant intégrée dans plusieurs accords internationaux, notamment (*i*) la Convention des Nations Unies sur les stocks chevauchants et les grands migrateurs et (*ii*) le Code de conduite de la FAO. Nous examinons de quelle façon l'application de ces accords modifiera les activités quotidiennes de nombreux organisations de gestion des pêches. Contrairement aux pratiques du passé, le manque de données scientifiques ne peut plus être invoqué pour éviter ou reporter la prise de mesures de conservation. Les futures stratégies de récolte s'appuieront sur des points de référence propres à un stock et sur des règles de décision établies à l'avance. Toutefois, d'autres recherches sont nécessaires pour quantifier les incertitudes associées aux définitions des points de référence et leur application pratique dans un cadre de gestion. De plus, les recherches futures seront axées sur des questions environnementales exigeant des données exhaustives, comme les effets de la pêche sur l'écosystème. La collecte de données demeurera une activité commerciale de base; les organismes doivent résoudre le du coût du maintien des archives de données communes et documentées à long terme.
[Traduit par la Rédaction]

Introduction

The precautionary approach has gained acceptance as a basis for fishery management (Garcia 1996; FAO 1995*a*, 1996), following the worldwide trend towards sustainable use of renewable resources (Garcia 1994). Collapses of economically important fisheries and widespread evidence of resource overexploitation and fleet overcapacity (FAO 1995*b*; Mace 1997) underlie the philosophical change embedded in this approach. Hence, past management practices must be modified to ensure the long-term viability of both fisheries and fishery resources. If implemented effectively, the precautionary approach will profoundly change the day-to-day operations of many national and international fisheries agencies. We provide a perspective on the nature of these changes and their implications for the future of fisheries management science.

Following Stephenson and Lane (1995), we use the term "fisheries management science" to refer to the broad integration of fisheries science, fisheries management, and management science. We discuss how the implementation of recent international agreements will alter the focus of these combined disciplines. The new directions will impact a broad range of activities, from basic data collection to the choice of harvest management strategies; we provide examples of these possible impacts. We begin by summarizing the main points in the agreements related to the precautionary approach. We then select key issues for further commentary and discussion. We conclude with an outlook for the future of fisheries management science, including priority areas for additional research.

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International agreements

The concept of the precautionary approach is included in several recent UN initiatives. Two of these, the Straddling Fish Stocks and Highly Migratory Fish Stocks Agreement (UN 1995), here termed "the Agreement", and the FAO Code of Conduct for Responsible Fisheries, are particularly important for fisheries management science. The Agreement was adopted by the UN General Assembly on 5 December 1995. However, the number of countries that have ratified the Agreement is not yet sufficient for it to be incorporated into the Law of the Sea. By contrast, the voluntary Code of Conduct for Responsible Fisheries has entered domestic legislation in a number of countries. Because of the carefully crafted overlap in these two instruments, many provisions of the Agreement are entering national legislation even without ratification.

Article 6 of the Agreement deals with the application of the precautionary approach, while Annexes I and II provide specific guidelines. We use these sections of the Agreement as our definition of the precautionary approach. The full text is available from the UN web site (www.un.org). Similarly, the Code of Conduct for Responsible Fisheries can be obtained from the FAO web site (www.fao.org).

Strictly, the Agreement pertains to straddling and highly migratory fish stocks. However, we consider the scope of the Agreement to include all fish stocks for the purpose of this perspective. More than 100 states participated in negotiations leading to the Agreement. Some of them, often coastal states, wanted to be extremely precautionary, while others, often distant water fishing nations, did not think that extreme precaution was necessary. It could therefore appear hypocritical if coastal states decided to be less precautionary with their domestic fisheries management than required by the Agreement. In fact, "improved management of domestic fisheries still has a long way to go" (FAO 1992, p. 2) and application of the precautionary approach is essential for ensuring long-term viability of fisheries (Mace 1997).

Many fisheries management processes are currently dominated by quantitative biological science. In a typical institutional setting, a committee of scientific experts provides advice to a decision-making management body (e.g., Parsons 1993; Caddy 1997) and much of the wording on the precautionary approach may appear directed to these experts. A potential danger is that the precautionary approach will be applied only to the analytical phase of the management process. Unfortunately, history indicates that decision makers sometimes fail to implement necessary measures despite repeated scientific warnings (Ludwig et al. 1993; Rosenberg et al. 1993; Holden 1994). Thus, the precautionary approach must be acknowledged at every step "of management, from planning through implementation, enforcement and monitoring to re-evaluation" (FAO 1995*a*, p. 7). The precautionary approach necessitates a different philosophical and practical approach to addressing uncertainty, regardless of the extent to which uncertainties can be quantified.

The precautionary approach

The essence of the precautionary approach is stated in Article 6.2: "States shall be more cautious when information is uncertain, unreliable or inadequate. The absence of adequate scientific information shall not be used as a reason for postponing or failing to take conservation and management measures" and improved methods are required for "dealing with risk and uncertainty" (Article 6.3*a*).

Article 6.2 implies a reversal of current practice in many fishery agencies and is often termed "the reversal of the burden of the proof" (FAO 1995*a*, pp. 4–5). Decision makers face strong economic, political, and social pressures resulting from scarce resources and fleet overcapacity. Traditionally, such pressures often forced decision makers to require substantive evidence of a conservation need before more stringent management measures were imposed (Gulland 1971; Sissenwine and Rosenberg 1993). For North Sea fisheries, for example, management measures might have prevented some conservation problems, but for political reasons, these measures could not be implemented before the problem actually occurred (Holden 1994, p. 113).

Evidence of a conservation need can be difficult to provide, particularly given the large uncertainties associated with most fishery data. Before recommending restrictive management measures, scientists generally want to ensure that their concerns are valid. For example, can the null hypothesis of no decline in fish stock abundance since the previous assessment be rejected against the alternative of declining abundance (Platt 1964; Peterman 1990). Thus, lack of adequate scientific evidence may have prevented or delayed the implementation of essential conservation measures (Gulland 1971).

The magnitudes of the uncertainties in fisheries management provide the principal justification for a precautionary approach. If there were no uncertainties and the consequences of various management actions were perfectly known, appropriate measures could be implemented without a precautionary approach. Uncertainty is related to risk. In the terminology of Francis and Shotton (1997), risk assessment involves the scientific formulation of advice to managers in a way that portrays potential consequences of uncertainty, while risk management involves accounting for uncertainty in the actual decision process. An extreme interpretation of the precautionary approach could be management to such a low risk that most fisheries would be closed. Conversely, management to a very high risk could lead to overexploitation at least to the point of economic extinction.

Harvest management strategies

Developed fisheries

For developed fisheries, stock-specific reference points (Caddy and Mahon 1995) provide the primary mechanism specified in the Agreement for applying precautionary approach. States shall "determine, on the basis of the best scientific information available, stock-specific reference points and the action to be taken if they are exceeded" (Article 6.3*b*). Two types of reference points are identified: "limit reference points set boundaries which are intended to constrain harvesting within safe biological limits within which the stocks can produce maximum sustainable yield", while "target reference points are intended to meet management objectives" (Annex II.2).

The explicit wording in Annex II reflects momentum in the scientific community towards management by reference points. To date, reference points have been used extensively

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as management tools in North America and Europe, although different agencies have adopted different criteria to meet their specific goals (Hilden 1993; Leaman 1993; Rivard and Maguire 1993). Reference points have been generally defined in terms of the fishing mortality rate F and expressed as targets rather than limits. However, the United States 602 Guidelines for fishery management plans require stock-specific overfishing definitions that establish maximum harvest levels (Sissenwine and Rosenberg 1993).

Once reference points have been established, "fishery management strategies shall ensure that the risk of exceeding limit reference points is very low" and "that target reference points are not exceeded on average" (Annex II.5). "The fishing mortality rate which generates maximum sustainable yield should be regarded as a minimum standard for limit reference points. For stocks which are not overfished, fishery management strategies shall ensure that fishing mortality does not exceed that which corresponds to maximum sustainable yield, and that the biomass does not fall below a predefined threshold. For overfished stocks, the biomass which would produce maximum sustainable yield can serve as a rebuilding target" (Annex II.7).

The Agreement clearly specifies F_{MSY}, the fishing mortality that can produce maximum sustainable yield (MSY), as a limit reference point that should not be exceeded. Therefore, fishing activities should be conducted such that the risk of exceeding F_{MSY} is very low (Caddy and McGarvey 1996). In addition, B_{MSY}, the biomass that can yield the long-term average MSY on application of F_{MSY}, is suggested as a rebuilding target for overfished stocks. A specific limit reference point for stock biomass is not defined. However, given F_{MSY} as a limit reference point, B_{MSY} could also be interpreted as a limit reference point.

With such strong statements in the Agreement, application of the precautionary approach might appear straightforward. The responsibility lies with the scientific sector to identify limit reference points, and the current biomass with short-term projections in relation to these reference points, both with associated uncertainties. The management agency then has the responsibility to develop an effective implementation plan, perhaps through the use of target reference points.[2] The plan must ensure that limit reference points are exceeded only with a low, preagreed probability.

If stock biomass is below or in danger of falling below the limit reference point B_{LIM}, then fishing activities should be curtailed to allow stock rebuilding. Conversely, if stock biomass is above B_{LIM}, then harvests can proceed as long as the risk of the stock biomass falling below B_{LIM} is very low, say on the order of 5%. For example, F could be 0 when the stock biomass is near or below B_{LIM} and increase linearly to the target fishing mortality rate for a stock biomass at or above the target reference point (ICES 1997*a*; Garcia 1996). A similar approach has been used successfully for Canadian Pacific herring fisheries, where B_{LIM} is defined as 25% of the estimated unfished average biomass. The exploitation rate is set at 20% of the forecast herring biomass. However, fisheries are closed if the biomass is below B_{LIM}, and exploitation rates are reduced if the biomass is marginally above B_{LIM} (Stocker 1993). Such harvest control rules have also recently been implemented for Icelandic cod, Atlanto-Scandian herring (Norwegian spring spawners), and North Sea herring (ICES 1997*b*).

The seeming simplicity of this approach belies two very real difficulties discussed below. The first is the uncertainty associated with establishing and measuring reference points. The second arises from practical difficulties in the development and application of management objectives. The Agreement and the Code of Conduct for Responsible Fisheries both stress the need to agree in advance on actions to be taken when reference points are approached or crossed. Without predetermined decision rules, immediate socio-politico-economic concerns often dominate, potentially delaying needed remedial measures (Hilborn and Luedke 1987; Holden 1994; Cook et al. 1997). Although the scientist must quantify and express the uncertainty in a meaningful way, the decision maker has the final responsibility to be precautionary. This may imply a change from current practice.

Fishery management decision makers are very rarely guided by a coherent set of quantified objectives. This lack of objectives is one of the concerns driving the concept of fisheries management science (Stephenson and Lane 1995). Generally, all interested parties share the long-term objectives of maintaining sustainable productive resources. Disputes usually arise over short-term political and economic objectives. The negotiation of specific fishery management objectives forces interested parties to state their objectives explicitly and establishes a process for conflict resolution. Periodic reviews of both science and management by independent experts can be a useful component of the negotiation process (Caddy 1997; Starr et al. 1998).

Data-poor situations

For some fisheries, the "best scientific information available" is simply inadequate for determining meaningful reference points and (or) current stock status with respect to such reference points. This situation can apply to new fisheries and to developed fisheries for which data on stock status are uninformative. For example, conflicting stock scenarios may be compatible with the available data (Richards 1991; Schnute and Hilborn 1993). In these cases, uncertainties will be higher than for comparable stocks with informative data sets, and management measures must be even more conservative to achieve a low risk of exceeding F_{MSY}. Hilborn and Walters (1992) make a strong argument for providing scientific advice even when data are scarce, perhaps because they share the view expressed in Walters and Maguire (1996, p. 126) that "Fisheries scientists view themselves as the good guys, seeking sustainable harvest regimes and providing conservative assessments as voices of moderation...". Indeed, when advice is not given, traditional fishery management agencies have generally taken the optimistic point of view. Under the precautionary approach, very conservative management measures are required when there is little scientific basis for advice.

In general, "provisional reference points may be established by analogy to similar and better-known stocks", along with "enhanced monitoring so as to enable revision of provisional reference points as improved information becomes available" (Annex II.6). However, reference points established by

[2] Although reference points have been applied mainly in the context of biological sciences, economic or social reference points could and should also be developed and adopted.

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analogy are not always appropriate. For example, western Atlantic Canadian cod stocks have collapsed under fishing mortality rates equal to or lower than those applied to eastern Atlantic cod stocks (e.g., Cook et al. 1997 versus Rivard and Maguire 1993). The reasons for such differences in resiliency have not been identified but are presumably related to population growth rates, fishery selectivity patterns in relation to fish age and maturity, and perhaps to the existence of natural refugia for specific age- or size-classes.

For new or exploratory fisheries, the Agreement specifies that "States shall adopt as soon as possible cautious conservation and management measures". These include "catch limits and effort limits" (Article 6.6). The guidelines in FAO (1995*a*) further elaborate the application of the precautionary approach in this context. For example, the use of area closures is recommended to limit risks, provide refuges, and allow experimental comparisons with fished areas. Increasingly, marine protected areas are advocated as a safeguard against overfishing (e.g., Walters and Maguire 1996; Walters and Parma 1996; Anonymous 1997). Protected areas are often perceived as a way to achieve conservation at smaller direct costs. However, the characteristics (location, size, etc.) necessary to make them effective tools for fishery management are the subject of much current debate (Carr and Reed 1993; Dugan and Davis 1993).

In some European fisheries, the term "precautionary TAC" (total allow catch) is used to denote catch limits on stocks for which analytical assessments have not been conducted. These TACs are typically determined by the quota required to maintain fishing fleet activities (Holden 1994, p. 124). Stocks subject to these catch limits may be fully or overexploited. Thus, precautionary TACs as defined above should not be confused with catch limits derived through application of the precautionary approach.

Uncertainty and risk

The magnitude of the uncertainties in fisheries management makes the precautionary approach necessary. As indicated above, if stock population dynamics and the consequences of various management actions were perfectly understood, the precautionary approach would not be necessary. The whole issue of risk and uncertainty is an expanding theme in fisheries management science addressed by several recent international conferences and review articles (e.g., Smith et al. 1993; Francis and Shotton 1997). With high-speed computers, more sophisticated techniques allow scientists to incorporate uncertainty in their stock assessments (e.g., Sullivan 1992; Schnute 1994; Schnute and Richards 1995; Punt and Hilborn 1997). Uncertainty applies both to the specification of reference points and to the implementation of management measures. In fact, the term "implementation uncertainty" (Rosenberg and Brault 1993) has been coined to reflect discrepancies between the actual and intended consequence of management actions.

Uncertainties tend to be particularly large in the identification of appropriate limit and target reference points, as well as in estimates of stock biomass that must be compared with these reference points. Reference points and biomass estimates are computed from mathematical models that relate the data observed on a stock to the assumed population dynamics. A model is necessarily a simplification of the underlying biological system. Experienced scientists will readily admit large uncertainties in key biological parameters, even when based on reasonably reliable input data. In particular, estimation of F_{MSY} requires a projection of future recruitment. The relationship between recruitment and parental stock size tends to be highly variable (Myers et al. 1995; Gilbert 1997; Richards et al. 1997) and at low stock sizes, where the risk is greatest, the relationship is often not known because of a lack of data for most stocks. However, in a precautionary approach, a cautious assumption should be made on how recruitment is related to spawning stock biomass (Francis 1997).

The concept of F_{MSY} is based on equilibrium conditions, assuming that the environment will continue to sustain the same yield. If the regime of environmental conditions and fish productivity changes, harvest rates based on previously calculated reference points may no longer be sustainable (Parsons 1993, p. 59; Caddy 1996). Standard assessment approaches cannot provide precautionary advice when conditions change outside the range of previous observations because they make inferences from historical data. The question of appropriate reference points for a variable environment has received limited scientific attention to date (Thompson 1994).

While modeling techniques have improved, current models have been rather unsuccessful in providing credible forecasts (Sharp 1995). Thus, most models simply fail to capture important features of the underlying dynamics and thereby underestimate actual uncertainties. An early application of risk analysis to fisheries problems (Hoenig et al. 1990; Restrepo et al. 1992), based on the best estimates of parameter variances available at the time, indicated a very low probability that the biomass would be as small as that estimated in subsequent assessments. Although this example may be an extreme case, it does illustrate why decision makers must acknowledge the possible reality of (presumed) low-probability events. In particular, outputs from a given model run should not be misinterpreted as reality. Rather, outputs from models with different structural assumptions should be compared. More weight can be placed on the outcome if management decisions are relatively insensitive to model selection (Punt and Hilborn 1997).

Unintended consequences can also occur in the implementation of management actions (Rice and Richards 1996). For example, discards of unwanted fish are a known problem associated with the introduction of individual transferable quotas in New Zealand (Annala et al. 1991). In eastern Canada, a groundfish minimum landing size regulation was introduced in the late 1980s, without corresponding changes in the regulated mesh size. Increased discard rates on juvenile fish during this period have now been documented (Sinclair et al. 1995; Myers et al. 1997). The intended benefit in terms of protection of juveniles and increased yield per recruit was not realized.

Impacts of fishing activities

The Agreement explicitly recognizes a large number of potential ecosystem impacts of fishing activities. These include "pollution, waste, discards, catch by lost or abandoned gear" and "catch of non-target species,...in particular endangered species" (Article 5*f*). States shall "assess the impacts of fishing" (Article 5*d*), "adopt...conservation and management measures for species...associated with or dependent upon the

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target stocks" (Article 5*e*), develop and use "selective, environmentally safe and cost-effective fishing gear and techniques" (Article 5*f*), and "protect biodiversity" (Article 5*g*).

These activities encompass a large and rapidly growing body of scientific literature, much of which is beyond the scope of this perspective. Traditionally, fisheries science has been based on a single-species approach to assessment and management. The need for multispecies approaches is widely recognized (Daan and Sissenwine 1991), but formal multispecies models are rarely used for management decisions (Gulland 1991). We anticipate that future progress will focus on broader ecosystem issues. In particular, research funds will likely be reallocated towards more strictly environmental concerns, such as bycatch of nontarget species (Hall 1996), habitat damage caused by mobile fishing gear (Auster et al. 1996), and general conservation benefits of marine protected areas.

Adverse impacts on fish stocks can sometimes result from natural phenomena. A classic example might be the 1914 rock slide on the Fraser River, British Columbia, that decimated many runs of sockeye salmon (Ricker 1950). The Agreement specifies that "States shall adopt conservation and management measures on an emergency basis to ensure that fishing activity does not exacerbate such adverse impact"(Article 6.7). More gradual impacts are those related to environmental changes or regime shifts (Beamish 1995; Steele 1996). The fisheries literature contains many debates on the relative importance of fishing and environmental factors as determinants of fish abundance (Sharp 1995). The precautionary approach clearly states that fishing must be curtailed if stock biomass falls below B_{LIM}, whatever the actual cause of stock declines.

Fishery data requirements

Data collection must remain a core business activity of any fishery management process because data form the basic currency for decision making. The Agreement specifies that "States shall improve decision-making for fishery resource conservation and management by obtaining and sharing the best scientific information available" (Article 6.3*a*) and shall "develop data collection and research programmes to assess the impact of fishing" (Article 6.3*d*). Specific guidelines for collecting and sharing data are given in Annex I of the Agreement. These describe the types of data to be collected, including catch, effort, discards, biological samples, and vessel specifications. Annex I also emphasizes the need for data verification. Appropriate agencies "shall compile data and make them available in a timely manner and in an agreed format to all interested States...while maintaining confidentiality of non-aggregated data, and should, to the extent feasible, develop database systems which provide efficient access to data" (Annex I.7.1).

The need to collect and share data is readily apparent for straddling and highly migratory fish stocks. Two or more states participate in the harvest of these stocks; meaningful stock assessment and management activities must consider data from all fisheries. We believe that the broad application of these data collection and sharing principles can advance the knowledge base for all fish stocks. Obviously, some information pertains to records of individual fishers and deserves to be protected as confidential. However, general dissemination of information may lead to broader benefits, and technological advances such as the world wide web can facilitate this process. For example, an educated public might "serve to marshal the political will needed to resist historical patterns of overexploitation" (Schnute and Richards 1994, p. 15). Furthermore, shared data are essential to a transparent decision-making process.

Data are expensive; the guidelines in Annex I are extensive and will be costly to implement. Given shrinking budgets, difficult decisions will be required to prioritize data collection and archival activities. For management purposes, the most important data are those needed to monitor the current progress of management measures, for example, the cumulative catch relative to an allowable limit. Data requirements for fisheries management science are more demanding. Analyses are usually based on long time series of information, whereby historical information can be as important as current data. Unfortunately, data older than a few decades tend to be regarded as unreliable because of poor documentation and storage standards. In other cases, data have been lost through institutional change or political upheaval (Mathews 1993). A system of shared data might mitigate against such disasters and provide more opportunities for rigorous analysis (Richards and Schnute 1998). However, real costs are associated with maintaining long-term data archives and lucid documentation.

The Agreement recognizes the need to establish agreed formats and standards to facilitate data sharing. International agencies such as FAO have already succeeded in sharing at least aggregated data on species catch and effort. Indeed, the Agreement names FAO as the agency to facilitate the "collection and dissemination of data" at the global level (Annex I.7.2). Modern relational databases can also help to guide and refine this process. Recent progress in the oceanographic community illustrates the potential to share data at an early stage. At a local level, fishing companies might decide to make some of their own data directly available to fishery agencies. For example, the British Columbia salmon marketing board (www.bcsalmon.ca) distributes one of the best databases on salmon catch statistics for Pacific Canada.

Outlook for fisheries management science

International instruments, such as the FAO Code of Conduct for Responsible Fisheries and the UN Agreement on Straddling Fish Stocks and Highly Migratory Fish Stocks, provide tools to fisheries management science. Provided that fisheries agencies are willing to use them, these tools can be extremely useful in designing and implementing successful fisheries management. Clearly, however, applying the intent of these agreements is just as important as enforcing the legal requirements. This will be difficult without a change in the attitudes of various interested parties and a change in the incentive systems underlying management processes.

A strict application of the reversal of the burden of proof could initiate a shift in attitudes of fishery management agencies. Thus, scientists could focus on quantifying and publicizing the uncertainties. Once uncertainties are more fully understood, incentives to collect additional reliable data would become clear. For example, additional data could provide support for less stringent management measures.

The shift in attitudes must apply on fishing boats, as well as in the meeting rooms. Currently, the fisher who catches the most, regardless of the means, is perceived as most successful

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(Mace 1997), although his potential contribution to resource collapse and overexploitation is proportionately greater than that of other fishers. Gavaris (1996) proposed a mechanism whereby conservation-oriented behaviors are rewarded, while nonconservation ones are penalized. His idea is to allocate recruits, rather than catches, and reward those fishery sectors that husband the resource for the common good. Penalties are assigned if fish are harvested before they have a chance to contribute to the spawning stock and future production.

Implementation of these changes may be insufficient unless there is also preagreement on the measures to implement when particular situations arise. Such preagreement requires the involvement of all interested parties in an open and transparent process, where the consequences of various measures are scientifically evaluated from a biological, ecological, economic, social, and political perspective. In such a system, the precautionary approach would be applied at every stage, from the development planning stage to the marketing of the products. One task of fisheries management science, but outside of traditional fisheries science, is to anticipate the effects of particular fishery management measures on fisher behavior. Systematic data collection would therefore cover the biological, economic, and sociological fields.

The development of fisheries management science, advocated by Stephenson and Lane (1995), incorporates biological, ecological, economic, social, and political aspects. Currently, the scientific field is dominated by the biological sciences. Although demands for biological advice have not decreased, more integrated advice is now required. Fisheries agency budgets have limited flexibility to respond to this need. Increasingly, other interested parties are sharing the financial support of this integrated advice. From a practical perspective, this implies major changes in resource leadership and accountability. In particular, we expect that the sequential approach currently applied, where the biology is conducted first and the other studies follow, will be replaced by a concurrent, parallel process with frequent cross-exchanges to ensure integrated advice.

In summary, we can identify a number of major steps in applying the precautionary approach to fisheries management science: (*i*) collect basic data on fish and fisheries, (*ii*) share these data to ensure a transparent process, (*iii*) establish reference points where possible, and establish conservative catch, effort, and capacity limits in data-poor situations, (*iv*) agree on decision rules that acknowledge uncertainty, and (*v*) initiate or enhance research to minimize impacts of fishing and other activities on the marine ecosystem. These steps are conducted by most management agencies to some extent. However, the challenge will be to apply them consistently and in a multidisciplinary context including social and economic concerns. For example, different agencies use different criteria for establishing reference points. Furthermore, decision rules rarely acknowledge full uncertainties, and uncertainties portrayed for one case may have a different interpretation than those derived for other cases.

The challenges here may appear daunting. However, some progress has already been made. International fisheries agencies such as ICES, the Northwest Atlantic Fishery Organisation (NAFO), the North Atlantic Salmon Conservation Organisation (NASCO), and the Intenational Baltic Sea Fishery Commission (IBSFC) are now debating these concepts and developing implementation plans. Thus, new directions for fisheries management science are becoming a reality.

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References

Anonymous. 1997. An approach to the establishment and management of marine protected areas under the Oceans Act, a discussion paper. Published by Communications Directorate, Department of Fisheries and Oceans, Ottawa, ON K1A 0E6, Canada. DFO/5444, Minister of Public Works and Government Services Canada 1997, Cat. No. Fs 23-307/1997E, ISBN 0-662-2529-5.

Annala, J.H., Sullivan, K.J., and Hore, A.J. 1991. Management of multispecies fisheries in New Zealand by individual transferable quotas. ICES Mar. Sci. Symp. **193**: 321–329.

Auster, P.J., Malatesta, R.J., Langton, R.W., Watling, L., Valentine, P.C., Donaldson, C.L.S., Langton, E.W., Shepard, A.N., and Babb, I.G. 1996. The impacts of mobile fishing gear on seafloor habitats in the Gulf of Maine (Northwest Atlantic): implications for conservation of fish populations. Rev. Fish. Sci. **4**: 185–202.

Beamish, R.J. (*Editor*).1995. Climate change and northern fish populations. Can. Spec. Publ. Fish. Aquat. Sci. No. 121.

Caddy, J.F. 1996. Regime shifts and paradigm changes: is there still a place for equilibrium thinking? Fish. Res. (Amst.), **25**: 219–230.

Caddy, J.F. 1997. Checks and balances in the management of marine fish stocks: organizational requirements for a limit reference point approach. Fish. Res. (Amst.), **30**: 1–15.

Caddy, J.F., and Mahon, R. 1995. Reference points for fisheries management. FAO Fish. Tech. Pap. No. 347.

Caddy, J.F., and McGarvey, R. 1996. Targets or limits for management of fisheries? N. Am. J. Fish. Manage. **16**: 479–487.

Carr, M.H., and Reed, D.C. 1993. Conceptual issues relevant to marine harvest refuges: examples from temperate reef fishes. Can. J. Fish. Aquat. Sci. **50**: 2019–2028.

Cook, R.M., Sinclair, A., and Stefansson, G. 1997. Potential collapse of North Sea cod stocks. Nature (Lond.), **385**: 521–522.

Daan, N., and Sissenwine, M.P. (*Editors*). 1991. Multispecies models relevant to management of living resources. ICES Mar. Sci. Symp. **193**.

Dugan, J.E., and Davis, G.E. 1993. Applications of marine refugia to coastal fisheries management. Can. J. Fish. Aquat. Sci. **50**: 2029–2042.

FAO. 1992. The state of food and agriculture 1992. World and regional reviews — marine fisheries and the Law of the Sea: a decade of change. FAO Agriculture Ser. No. 25.

FAO. 1995*a*. Precautionary approach to fisheries. Part 1: Guidelines on the precautionary approach to capture fisheries and species introductions. FAO Fish. Tech. Pap. No. 350/1.

FAO. 1995*b*. The state of world fisheries and aquaculture. FAO, Rome.

FAO. 1996. Precautionary approach to fisheries. Part 2: Scientific papers. FAO Fish. Tech. Pap. No. 350/2.

Francis, R.I.C.C. 1997. Comment: How should fisheries scientists and managers react to uncertainty about stock–recruit relationships. Can. J. Fish. Aquat. Sci. **54**: 982–983.

Francis, R.I.C.C., and Shotton, R. 1997. "Risk" in fisheries management: a review. Can. J. Fish. Aquat. Sci. **54**: 1699–1715.

Garcia, S.M. 1994. The precautionary principle: its implications in capture fisheries. Ocean Coastal Manage. **22**: 1195–1207.

Garcia, S.M. 1996. Stock–recruitment relationships and the

© 1998 NRC Canada

precautionary approach to management of tropical shrimp fisheries. Mar. Freshwater Res. **47**: 43–58.

Gavaris, S. 1996. Population stewardship rights: decentralized management through explicit accounting of the value of uncaught fish. Can. J. Fish. Aquat. Sci. **53**: 1683–1691.

Gilbert, D.J. 1997. Towards a new recruitment paradigm for fish stocks. Can. J. Fish. Aquat. Sci. **54**: 969–977.

Gulland, J.A. 1971. Science and fishery management. J. Cons. Cons. Int. Explor. Mer, **33**: 471–477.

Gulland, J.A. 1991. Under what conditions will multispecies models lead to better fisheries management? ICES Mar. Sci. Symp. **193**: 348–352.

Hall, M.A. 1996. On bycatches. Rev. Fish Biol. Fish. **6**: 319–352.

Hilborn, R., and Luedke, W. 1987. Rationalizing the irrational: a case study in user group participation in Pacific salmon management. Can. J. Fish. Aquat. Sci. **44**: 1796–1805.

Hilborn, R., and Walters, C.J. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall. New York.

Hilden, M. 1993. Reference points for fisheries management: the ICES experience. *In* Risk evaluation and biological reference points for fisheries management. *Edited by* S.J. Smith, J.J. Hunt, and D. Rivard. Can. Spec. Publ. Fish. Aquat. Sci. No. 120. pp. 59–65.

Hoenig, J.M., Baird, J.W., and Restrepo, V.R. 1990. Describing the risk associated with a given quota when the stock assessment is based on sequential population analysis. CAFSAC Res. Doc. No. 90/75.

Holden, M. 1994. The common fisheries policy. Fishing News Books, Oxford, U.K.

ICES. 1997*a*. Report of the comprehensive fishery evaluation working group. ICES C.M. 1997/Assess: 15.

ICES. 1997*b*. Report of the ICES Advisory Committee on Fishery Management, 1996. ICES Coop. Res. Rep. No 221, parts 1 and 2.

Leaman, B.M. 1993. Reference points for fisheries management: the western Canadian experience. *In* Risk evaluation and biological reference points for fisheries management. *Edited by* S.J. Smith, J.J. Hunt, and D. Rivard. Can. Spec. Publ. Fish. Aquat. Sci. No. 120. pp. 15–30.

Ludwig, D., Hilborn, R., and Walters, C. 1993. Uncertainty, resource exploitation, and conservation: lessons from history. Science (Washington, D.C.), **260**: 17–36.

Mace, P.M. 1997. Developing and sustaining world fisheries resources: the state of the science and management. *In* Developing and sustaining world fisheries resources: the state of the science and management, SecondWorld Fisheries Congress, Brisbane 1996. *Edited by* D.A. Hancock, D.C. Smith, A. Grant, and J.P. Beumer. CSIRO, Melbourne. pp. 1–20.

Mathews, C.P. 1993. On preservation of data. Naga, ICLARM Q. **16**(2–3): 39–41.

Myers, R.A., Bridson, J., and Barrowman, N.J. 1995. Summary of worldwide spawner and recruitment data. Can. Tech. Rep. Fish. Aquat. Sci. No. 2024.

Myers, R.A., Hutchings, J.A., and Barrowman, N.J. 1997. Why do fish stocks collapse? The example of cod in Atlantic Canada. Ecol. Appl. **7**: 91–106.

Parsons, L.S. 1993. Management of marine fisheries in Canada. Can. Bull. Fish. Aquat. Sci. No. 225.

Peterman, R.M. 1990. Statistical power analysis can improve fisheries research and management. Can. J. Fish. Aquat. Sci. **47**: 2–15.

Platt, J.R. 1964. Strong inference. Science (Washington, D.C.), **146**: 347–352.

Punt, A.E., and Hilborn, R. 1997. Fisheries stock assessment and decision analysis: the Bayesian approach. Rev. Fish Biol. Fish. **7**: 35–63.

Restrepo, V.R., Hoenig, J.M., Powers, J.E., Baird, J.W., and Turner, S.C. 1992. A simple simulation approach to risk and cost analysis, with applications to swordfish and cod fisheries. Fish. Bull. U.S. **90**: 736–748.

Rice, J.C., and Richards, L.J. 1996. A framework for reducing implementation uncertainty in fisheries management. N. Am. J. Fish. Manage. **16**: 488–494.

Richards, L.J. 1991. Use of contradictory data sources in stock assessments. Fish. Res. (Amst.), **11**: 225–238.

Richards, L.J., and Schnute, J.T. 1998. A strategy for advancing stock assessment. *In* Reinventing fisheries management. *Edited by* T.J. Pitcher, P.J.B. Hart, and D. Pauly. Chapman and Hall, London, U.K. pp. 399–406.

Richards, L.J., Schnute, J.T., and Olsen, N. 1997. Visualizing catch-age analysis: a case study. Can. J. Fish. Aquat. Sci. **54**: 1646–1658.

Ricker, W.E. 1950. Cyclic dominance among the Fraser sockeye. Ecology, **31**: 6–26.

Rivard, D., and Maguire, J.J. 1993. Reference points for fisheries management: the eastern Canadian experience. *In* Risk evaluation and biological reference points for fisheries management. *Edited by* S.J. Smith, J.J. Hunt, and D. Rivard. Can. Spec. Publ. Fish. Aquat. Sci. No. 120. pp. 31–57.

Rosenberg, A.A., and Brault, S. 1993. Choosing a management strategy for stock rebuilding when control is uncertain. *In* Risk evaluation and biological reference points for fisheries management. *Edited by* S.J. Smith, J.J. Hunt, and D. Rivard. Can. Spec. Publ. Fish. Aquat. Sci. No. 120. pp. 243–249.

Rosenberg, A.A., Fogarty, M.J., Sissenwine, M.P., Beddington, J.R., and Shepherd, J.G. 1993. Achieving sustainable use of renewable resources. Science (Washington, D.C.), **262**: 828–829.

Schnute, J.T. 1994. A general framework for developing sequential fisheries models. Can. J. Fish. Aquat. Sci. **51**: 1676–1688.

Schnute, J.T., and Hilborn, R. 1993. Analysis of contradictory data sources in fish stock assessments. Can. J. Fish. Aquat. Sci. **50**: 1916–1923.

Schnute, J.T., and Richards, L.J. 1994. Stock assessment for the 21st century. Fisheries (Bethesda), **19**(11): 10–16.

Schnute, J.T., and Richards, L.J. 1995. The influence of error on population estimates from catch–age models. Can. J. Fish. Aquat. Sci. **52**: 2063–2077.

Sharp, G.D. 1995. It's about time: new beginnings and old good ideas in fisheries science. Fish. Oceanogr. **4**: 324–341.

Sinclair, A.F., Chouinard, G., Swain, D., Nielsen, G., Hanson, M., Currie, L., Hurlbut, T., and Hebert, R. 1995. Assessment of the southern Gulf of St. Lawrence cod stock, March 1995. DFO Atl. Fish. Res. Doc. No. 95/39.

Sissenwine, M.P., and Rosenberg, A.A. 1993. Marine fisheries at a critical juncture. Fisheries (Bethesda), **18**(10): 6–14.

Smith, S.J., Hunt, J.J., and Rivard, D. (*Editors*). 1993. Risk evaluation and biological reference points for fisheries management. Can. Spec. Publ. Fish. Aquat. Sci. No. 120.

Starr, P.J., Annala, J.H., and Hilborn, R. 1998. Contested stock assessment: two case studies. Can. J. Fish. Aquat. Sci. **55**: 529–537.

Steele, J.H. 1996. Regime shifts in fisheries management. Fish. Res. (Amst.), **25**: 19–23.

Stephenson, R.L., and Lane, D.E. 1995. Fisheries management science: a plea for conceptual change. Can. J. Fish. Aquat. Sci. **52**: 2051–2056.

Stocker, M. 1993. Recent management of the British Columbia herring fishery. *In* Perspectives on Canadian marine fisheries management. *Edited by* L.S. Parsons and W.H. Lear. Can. Bull. Fish. Aquat. Sci. No. 226. pp. 267–293.

Sullivan, P.J. 1992. A Kalman filter approach to catch-at-length analysis. Biometrics, **48**: 237–257.

Thompson, G.G. 1994. A general diffusion model of stock–recruitment systems with stochastic mortality. ICES C.M. 1994/T:18.

UN. 1995. Agreement for the implementation of the provisions of United Nations Convention on the Law of the Sea of 10 December

© 1998 NRC Canada

1982 relating to the conservation and management of straddling fish stocks and highly fish stocks. United Nations General Assembly Document A/CONF.164/37 (8 September 1995), New York.

Walters, C., and Maguire, J.J. 1996. Lessons for stock assessment from the northern cod collapse. Rev. Fish Biol. Fish. **6**: 125–137.

Walters, C., and Parma, A.M. 1996. Fixed exploitation rate strategies for coping with effects of climate change. Can. J. Fish. Aquat. Sci. **53**: 148–158.

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Conference Canadienne de la recherche sur les peches (CCRP)

Edmonton (Alberta)
les 8–10 janvier 1999

Les principaux thèmes abordés lors de la **Conférence de 1999** seront :

(1) Les impacts de l'utilisation des terres sur les poissons de rivière et leurs habitats

(2) Les impacts des disrupteurs endocrinaires et des contaminants

(3) Changements climatiques et écosystémiques

(4) Applications innovatrices des études génétiques dans la gestion des pêches

(5) **Session Conjointe CCRP/SCL** : (sera annoncée ultérieurement)

Des contributions reliées aux thèmes principaux sont particulièrement sollicitées, mais des contributions sur d'autres thèmes reliés aux sciences halieutiques et à la biologie des habitats aquatiques sont également bienvenues.

La **DATE LIMITE pour la soumission des résumés est le 11 septembre 1998**. Veuillez les soumettre au :

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Relationships between sunspots and sea stars (O)
Gretzky*, W., and J. Villeneuve. Department of Epidemiology, Eastern University, Yoho, Saskatchewan

Sea stars shine increasingly brightly as the sunspot cycle progresses...

Could be poster; theme 3

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Predation par les euphausiaces sur les bebes phoques (O)
Villeneuve*, J., et W. Gretzky. Departement de planctonologie, Université de Trois Pistoles, Trois Pistoles (Québec)

Une augmentation subite de la mortalité des bébés phoques s'est avérée...

Pourrait être affiche; thème 3

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David I. Gibson

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More than 80 keys leading to the identification of more than 220 species of trematode parasites of Canadian fishes and diagnoses of more than 80 family–group taxa and 130 genera are given. Each genus is illustrated. For each species a Canadian host list, locality data, and any relevant remarks are included. Visit http://www.nrc.ca/cisti/journals/40083/133to136.html at the NRC Research Press Web to view a short chapter of this book.

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Numerical Methods in Atmospheric and Oceanic Modelling

The André J. Robert Memorial Volume

Charles A. Lin, René Laprise and/et Harold Ritchie (Editors/Directeurs scientifiques)

634 pages
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